

## A Review of Recent Knowledge of the Ecology of the Main Vectors of Trypanosomiasis\*

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*In this survey of recent ecological research on the main vectors of trypanosomiasis in those countries of East, Central and West Africa that are not predominantly French-speaking, the authors, after outlining the distribution of tsetse flies and the type of country in which they occur, discuss the direct and indirect effects of climate on these insects—particularly on their physiological water balance and on pupal fat reserves—and their recent advances into new areas. They review the considerable work that has been done on the resting habits and breeding-sites of different Glossina species, knowledge of which is important for effective control, and research on predators of pupae and adult flies and on the feeding activity of tsetse flies. Means of assessing populations and various factors affecting the size and nutritional status of tsetse flies are also discussed, as is the effect on the fly population of artificial changes in the habitat. Finally, a plea is made for a revision of present methods of land use and stock management, if full advantage is to be taken of achievements in fly control.*

The following review covers the ecological research work on the tsetse flies of East, Central and West Africa carried out in countries other than those predominantly French-speaking during the past ten years; where necessary, however, we have mentioned earlier work because most of our present knowledge is based upon it.

By East Africa is meant Kenya, Uganda, Tanganyika, the Protectorate of Zanzibar; by Central Africa, the Federation of Rhodesia and Nyasaland, Mozambique and the southern two-thirds of Angola, the Bechuanaland Protectorate and the Republic of South Africa (Zululand); by West Africa, the Federation of Nigeria, Ghana and part of the Sudan.

Some of the more noteworthy advances in tsetse-fly research include Weitz's serological method of identifying tsetse-fly blood meals which, with Jackson's assistance in the early stages, made it possible to throw more light on the host-fly relationships.

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The West African Institute for Trypanosomiasis Research carried out a comprehensive study of the ecology of *G. palpalis* in Northern Nigeria, and also studied some of the species found in Southern Nigeria.

Glasgow's, and later Isherwood's, studies of the feeding and resting habits of different flies, and Bursell's work on water balances and fat contents of the adults and pupae go a long way to explain the effect of climate on the range and habitats of different tsetse-fly species. Then there is Ford & Leggate's review of the trypanosome infection rates in *Glossina* in relation to geographical and climatic distribution; also Harley and Pilson's studies on the effect on *G. morsitans* of artificial changes in its habitat in Uganda, Langridge's experiment in Kenya on the effect of light intensity on the breeding-sites of *G. austeni* and Parsons' investigations of the breeding-sites of *G. pallidipes*. The work carried out over the past ten years by the East African Trypanosomiasis Research Organization, much of which has been covered by Harley's review on the entomological work done by the officers of that organization up to 1960, is invaluable but unfortunately space does not permit of it all being included here.

The work by Jackson, Ford, Southon, and Renison et al. on the assessment of populations pointed

the way to improvements in the old methods of survey and fly population studies.

Much of the information in this review is virtually that contained in the authors' summaries, as it was not possible to delve deeply into any particular aspect but merely to indicate modern trends in this field of research.

Recently great advances have been made in the practical application of ecological knowledge to the control of *Glossina* and the disease it transmits, which have led to improved techniques in survey methods, assisted by traps and attractants. Also the study of the movement of flies and of their resting habits has led to the development of more economical and better methods of control, particularly with insecticides.

#### DISTRIBUTION OF TSETSE FLIES

According to Ford,<sup>1</sup> the southern limits of *Glossina* distribution in Africa lie north of a line drawn from Benguela in Angola to Durban in South Africa. The northern limits are roughly a line from Dakar 15°N on the west coast across to Mogadiscio on the east coast. A few isolated areas occupied by some species of the genus may be found up to 12°N on the eastern side. The main factors which limit the distribution of tsetse flies are: climate, soil and vegetation, human population and the distribution of wild game animals. The effect of vegetation is particularly noticeable in the more northerly parts of the range of *Glossina*, leading to its restriction to the vicinities of watercourses—this is so even with *G. morsitans*, which elsewhere is regarded as a woodland savannah species.

This review covers the following tsetse species:

	West Africa	Central Africa	East Africa
<i>Glossina morsitans morsitans</i> Westwood	—	+	+
<i>G. morsitans orientalis</i> Vanderplank	—	+	+
<i>G. morsitans submorsitans</i> Newstead	+	—	+
<i>G. austeni austeni</i> Newstead	—	+	+
<i>G. austeni mossurizensis</i> Santo Dias	—	+	—
<i>G. pallidipes</i> Austen	—	+	+
<i>G. brevipalpis</i> Newstead	—	+	+
<i>G. swynnertoni</i> Austen	—	—	+
<i>G. fuscipes fuscipes</i> Newstead	—	—	+
<i>G. palpalis martinii</i> Zumpt	—	+	+
<i>G. palpalis palpalis</i> Robineau-Desvoidy	+	—	—
<i>G. fusca</i> Walker	+	—	+
<i>G. nigrofusca</i> Newstead	+	—	—

<sup>1</sup> Data sent to us (1962) for inclusion in this paper; see also the article by Ford on page 653 of this issue.

	West Africa	Central Africa	East Africa
<i>G. fuscipleuris</i> Austen	—	+	+
<i>G. haningtoni</i> Newstead & Evans	—	—	+
<i>G. longipennis</i> Corti	—	—	+
<i>G. tachinoides</i> Westwood	+	—	—
<i>G. longipalpis</i> Wiedemann	+	—	—
<i>G. medicorum</i> Austen	+	—	—

On the basis of Vanderplank's (1949) classification, the eastern race of *G. morsitans orientalis* occupies Mozambique, the eastern fly-belts of Northern Rhodesia and the Zambezi valley in Southern Rhodesia; the western belt of Northern Rhodesia and Bechuanaland contain *G. morsitans morsitans*.

The separation of the Angola *morsitans* into a third race, *congolensis*, is not yet established and the species is shown as *G. morsitans morsitans* in the most recent maps from Angola (Ford, *op. cit.*).

*G. morsitans submorsitans* extends from north-eastern Uganda, through a small area in north-west Kenya to Nigeria and Guinea.

In Central and East Africa, *G. morsitans* is one of the most important vectors of human and animal trypanosomiasis (Vanderplank, 1949), but in West Africa its importance is as a vector of animal trypanosomiasis only. Although *T. rhodesiense* infections have been known (Lester, 1933), the prime causative organism of West African human trypanosomiasis is *T. gambiense*, which is not normally carried by *G. morsitans*.

Much of the country infested with *G. morsitans orientalis* also carries *G. brevipalpis*, *G. austeni* and *G. pallidipes*. Pires, da Silva & Teles e Cunha (1950) have described the comparative ecology of these four species in the Sitatonga hills in western Mozambique. The four species, although overlapping to some degree, show relatively precise attachment to the main vegetation types of the area.

*G. brevipalpis* is principally dependent on mesophytic forest dominated by large trees of *Khaya nyasica*, *Chrysophyllum fulvum*, *Newtonia buchanani*, etc., with an understorey of shrubs hung with lianas. It also makes use of riverine thicket with *Ficus*, *Kigelia*, *Trichilia*, etc.

*G. austeni* is found in the margins of these forest types and in secondary dense thickets, as is *G. pallidipes*, although the latter penetrates into more xerophytic vegetation, particularly on formerly cultivated land.

Although there is considerable overlap of the habits of *G. brevipalpis*, *G. austeni* and *G. pallidipes* in Central and East Africa, only the last overlaps *G. morsitans* to any degree.

Closely linked with climate and human settlement, the most obvious limiting feature of *Glossina* distribution in Central Africa is the Kalahari desert, which is not penetrated by tsetse flies except near its northern limit where drainage of the Okovango river creates a habitat for *G. morsitans* in edaphically controlled vegetation on the edges of flood channels (Ford, *op. cit.*).

In East Africa the main limiting factors are also deserts such as occur in northern Kenya and north-western Uganda, and highlands at altitudes of more than 6000 feet (1800 m) above sea level, such as those which occur in Central Kenya.

A unique feature of Central African *G. morsitans* is its occupation of "mopane" (*Colophospermum mopane*) savannah woodlands; these occur in a broad band some 200 miles (320 km) wide, not quite reaching the east or west coasts from Central Mozambique to Angola, with an extension to the north-east in the Luangwa valley in Northern Rhodesia.

Of interest also is the occupation by *G. morsitans* of the ant-hill thicket and *Acacia* woodland country of Ankole in Uganda.

Also peculiar to Central Africa are the *Baikiaea* woodlands occurring in soils derived from Kalahari sands; the apparent unsuitability of this type of woodland as a *G. morsitans* habitat is a subject needing further attention.

The great *Brachystegia* woodlands of East Africa find their southern limit in Central Africa and Angola. The presence of species such as *Marquesia* suggests that *Brachystegia* woodland and its attendant *G. morsitans* are invading country formerly occupied by rain forests. The distribution of *G. morsitans* in Angola is evidence that at one time this tsetse fly occupied a more extensive area south of the Congo forest than at present (Ford, *op. cit.*).

In Nigeria there is a definite difference between the ecology of *G. morsitans submorsitans* in the Sudan Zone and that in the Guinea Zone.

*The Sudan Zone.* In this region, *G. morsitans* inhabits the third zone described below for *G. tachinoides*. Its ecology has been considerably investigated by several workers based on the now defunct research station at Gadau (Nash, 1937; etc.). More recent observations in connexion with control schemes have been made by MacLennan & Kirkby (1958), Kirkby & Blasdale (1960) and Kernaghan (unpublished data).

*The Guinea Zone.* The great difference here is that *G. morsitans submorsitans* is an inhabitant of the

woodland savannahs, closely resembling in habit *G. morsitans morsitans* of Central and East Africa. In view of the economic implications associated with the potential development of a major cattle industry, considerable exploration of the distribution of *G. morsitans* has been, and is still being, carried out, largely by the Tsetse Control Unit of the Northern Nigerian Ministry of Animal Health and Forestry. Their more recent results will be published in due course (personal communication from Mr K. J. R. MacLennan).

Originally thought to be confined in relatively small belts in Northern Nigeria, *G. morsitans* has now been shown to be much more widespread, covering vast tracts of country. Altogether, it is estimated that about 50 000 square miles (120 000 km<sup>2</sup>) of country are infested (MacLennan, 1958), but it is likely that this figure may be increased. This wider distribution is in part due to the previous lack of widespread surveys, now being remedied, and partly to undoubted recent advances or colonization of hitherto uninfested country. Generally, the presence of *G. morsitans* is incompatible with a high human population density. Human depopulation by slaving, disease and administrative moves has allowed the vegetation to revert back to something approaching its former state, creating potential *G. morsitans* habitats. What is not clear is what has given the recent impetus to the fly to start spreading. The potential sites were available before 1952, but only then did the movement, which is still continuing, become obvious. There may be a seasonal cycle of favourable and unfavourable climatic periods involved, but it has not been elucidated. Such a cycle would imply a future recession, back towards the original limits, where presumably the fly can withstand the unfavourable part of the cycle. Wilson (1958) gives some account of these advances. Recessions have taken place, due mainly to human population movements into infested areas. In such cases, the distribution of communities and their resulting zones of influence, rather than the over-all population density figure, is more important.

*G. pallidipes* in East Africa is most widespread in Kenya, where it is of great economic importance as a vector of animal trypanosomiasis. Recent investigations, however, by Willett (1958), Ashcroft (1958b), Ashcroft & Hilton (1958) and Heisch et al. (1958) have indicated that it appears to be implicated in the transmission of *T. rhodesiense* in Western Kenya and the Busoga district of Uganda.

*Glossina austeni mossurizensis* in the Sitatonga hills has been given separate subspecific status by Santos Dias (1956), but *G. austeni*, occurring on the Mozambique coast, extends from the Swaziland border in South Africa in a number of small isolated belts to southern Somalia in the north (Moggridge, 1936b). It is sometimes associated with *G. brevipalpis* in these belts, and occurs also on the island of Zanzibar.

Johns (1950) studied the vegetational requirements of *G. austeni* on the island of Zanzibar and found that it had a tendency to disperse from the thicker forest areas during dry spells. However, whereas *G. austeni* does not occur more than 150 miles (240 km) inland from the East African coast, *G. brevipalpis* is much more widely distributed, reaching from St Lucia in Natal (du Toit & Kluge, 1956) through Mozambique to the Southern Rhodesian border, into Nyasaland and thence westwards across Northern Rhodesia into the eastern Congo and northwards through Kenya into Uganda. For the most part it is associated with *G. morsitans* in Central Africa, although occupying pockets of riverine gallery forest, but in Nyasaland it occurs in ant-hill thickets near the lake shore or in forested gullies in *Brachystegia* woodland under high rainfall conditions in the north (Mitchell & Steele, 1956). Somewhat surprisingly, *G. pallidipes* is not found in Nyasaland.

*G. swynnertoni* inhabits large areas of hardpan scrub country in northern Tanganyika and extends also into a small part of the south-western corner of Kenya Masailand but does not occur in Uganda at all. It is an important vector of both human and animal trypanosomiasis.

*G. fuscipes fuscipes* (formerly *G. palpalis fuscipes*) occurs on the shores and islands of Lake Victoria and along the rivers running into it, but in Uganda it is also found along the White Nile and its swamps and tributaries. It is a vector of human sleeping-sickness but does not appear to be of great importance as a carrier of animal trypanosomiasis.

*G. palpalis martinii* is found only in the extreme north-west of Northern Rhodesia on the lacustrine fringes of Lakes Tanganyika and Mweru, where until recently it was an important vector of human sleeping-sickness. Tsetse flies of the *palpalis* group have never been recorded in any drainage system entering the Indian Ocean; the *G. palpalis*-group fly-belts of northern Angola belong to the West African zone, where this species is extremely widespread. The subspecies *angolensis* and *gambiensis* are not dealt with in this review.

*G. palpalis palpalis* is extremely widespread in West Africa, ranging (in Nigeria) from the coast northwards to approximately latitude 10°30'N. Detailed ecological studies have been made by Nash & Page (1953) very close to its northern limit, and by Page (1959b) further south (latitude 6°46'N), where there is a much more humid climate, not subject to the desiccating effect of the dry season wind, the harmattan, which has such a profound effect on *Glossina* generally in the northern areas.

Low pregnancy rates of *G. palpalis* may explain, at least in part, the low densities of this fly commonly found in the forest belts of West Africa, despite its wide distribution (Jordan, 1962b).

Ecological studies have been made by the West African Institute of Trypanosomiasis Research on some of the tsetse-fly species found in Southern Nigeria and have been summarized by Jordan (1960a).

*G. fusca* inhabits the forests of western Uganda, extending through the Congo to Nigeria and Guinea and *G. nigrofusca* occurs in Southern Nigeria and Guinea. Attention has been drawn recently to their potentialities as vectors of disease, based on wild fly trypanosome infection rates (Page, 1959c).

The ecology of four tsetse-fly species of the *fusca* group was studied near the Ugabobigha field station of the West African Institute for Trypanosomiasis Research in Southern Nigeria (Jordan, 1962a). He found that *G. tabaniformis* Westw. and *G. nigrofusca* Newst. occurred in "lowland rain forest" and *G. medicorum* Aust. in forest outliers in "derived savannah"; *G. fusca* was present in both habitats. Meteorological records showed that the climate in the rain forest was cooler and more humid than in the forest outliers, where in turn it was more equable than in the savannah. The distribution of the four species, each with its own range of tolerance, was thought to be largely determined by the climatic conditions within the various habitats.

In Ghana, *G. nigrofusca* has been reported to penetrate savannah (Nash, 1948).

*G. fuscipleuris* is to be found in the forests of western Uganda and along the Mara and Migori rivers of Kenya and is not of great importance, except perhaps in Uganda.

*G. hanningtoni*, like *G. fusca*, occurs in some of the forested parts of western Uganda and West Africa. At present it is not known to be a serious vector of human or animal trypanosomiasis.

*G. tachinoides* is an extremely widespread species in West Africa, but is predominantly known as a

northern form, through its ability to flourish in areas subject to considerable severity of climate. In such areas it is often associated with *G. morsitans*, but in the more temperate area of the Guinea savannahs it has not adopted the latter's habit of living freely in the open woodland. It remains restricted, generally speaking, to the riverine fringing forest, and mixed populations of *G. tachinoides* and *G. palpalis* (the latter almost always predominating) are common. The southern distribution is still not known perfectly, as it has a great facility for living in infinitesimal density, and for utilizing abnormal breeding-sites. Jordan (1960a) notes that only three specimens were caught in three years of intensive fly-rounds in the south; while in the central Niger valley, only one specimen was caught in 18 months of observation (R. J. Kernaghan—personal record). At this level the species cannot be of economic importance, but cases have been known where the effect of control measures aimed at *G. palpalis* has been to produce a new complication in the form of a population of *G. tachinoides* of significant proportions (Kernaghan, 1961).

The ecology of *G. tachinoides*, where it is a dominant species (i.e., approximately 10°30'N to 13°N and mainly included in the Sudan savannah), has been briefly described by Kernaghan (1960, 1961), who divides its river habitats into three zones. The first zone, in the southern part of the range, is composed of river sources and associated complexes of tributaries, very similar in form and vegetation to that described by Nash & Page (1953) in connexion with *G. palpalis* in the North Guinea savannah. The second zone, into which the first merges, has river reaches with wide sandy beds (full only in the late wet season) and a light vegetation on their banks. It is not favourable to *G. tachinoides*, except where an artificial habitat (usually plantations of mango trees) has been allowed to develop. There is always a high density of human population. In the third zone the rivers are completely changed in character. The river bed becomes narrow, breaking up into numerous channels and meandering through a flood plain, usually several miles wide and heavily wooded. The human population is dense up to the edge of the flood plain, which, owing to the seasonal floods, is not inhabited. Game, particularly warthog (*Phacochoerus africanus*) is relatively common. This zone, in which *G. morsitans* is almost always present, probably provides the optimum habitat for *G. tachinoides*. It has been described in detail by Nash (1937; and associated papers) and by

MacLennan & Kirkby (1958). This division into the zones described was originally based on observations on the Hadejia river system, a principal feeder of Lake Chad, but it applies equally well elsewhere.

There have been no ecological studies of equivalent intensity carried out since Nash's work in the third zone in the period 1935-42. It is to be remembered that he was largely concerned with "forest islands" in the flood plain, rather than in the main river channel, which elsewhere has been found to be the primary habitat.

The use of abnormal or man-made habitats by this fly must be noted. For instance, overhanging rocks in a stream bed, usually with a pool of water in association, may provide a suitable microclimate even though no vegetation is near. In one case, noted by Davies, breeding was taking place in the dry season among the roots of grass (*Chloris* sp.) and associated rocks in a dry stream bed devoid of any other vegetation (Glover, 1961b). This, of course, has important implications, as the aim of tsetse-fly control methods using clearing of the woody vegetation is to replace the latter by grass. The site in question had been cleared a year or so previously in connexion with a control scheme; obviously, in certain circumstances breeding may carry on in spite of control measures. Sacred groves, such as are found in so-called "pagan" areas, often hold a small population of *G. tachinoides*, while in a more southern district (Southern Guinea Savannah Zone), where *G. palpalis* predominates, a population of *G. tachinoides* was found in direct association with a small village. The main breeding-site (dry season) was the floor of a small thatched market stall, but pupae were also found at the base of a hut wall, below the low overhanging eaves, and near mango trees which were close by. The nearest stream was 150 m distant, but a variety of food hosts was available all the time (Kernaghan, 1960).

Plantations of mango trees—particularly, as noted above, in the second zone—are extremely important. They form perfect habitats, with their outer branches touching the ground, leaving a clear open space around the trunks. This lateral insulation is often reinforced by hedges put up by the owners as a protection against goats. They usually stand close to a river, and often irrigated farming is carried on among them, providing ideal humidity conditions. There are several records of trypanosomiasis epidemics, both human and animal, which have been due entirely to this artificial habitat.

*G. longipalpis* is found only in areas with a rainfall of more than 45 inches (1.14 m) *per annum*, i.e., mainly in the Southern Guinea Savannah Zone. In the more northern parts of its range, it appears to have a somewhat discontinuous distribution. Relatively high densities may be found, as noted by Davies (Glover, 1961b). More intensive surveys may show that it is more ubiquitous than has been thought and the economic importance of this fly has only recently been appreciated. In many ways its habits are similar to those of *G. pallidipes* in East Africa.

*G. medicorum*, occurring in Nigeria and Guinea, prefers riverine vegetation and forest islands in savannah and does not inhabit the main forest belt. Attention has recently been drawn to its economic importance as a vector of animal trypanosomiasis, as infection rates in wild populations examined were high (Page, 1959b).

#### CLIMATE

Rainfall in the tsetse-fly infested zones of Central Africa varies from 80 inches (2.03 m) *per annum* in the *G. brevipalpis* belts to 16 inches (406 mm) in the *G. morsitans* belt of the Bechuanaland Protectorate. Temperatures vary from maxima of 40°C to just under 0°C and these temperature limits are repeated in some areas in a wide diurnal range which may exceed 22°C in winter months (Ford<sup>1</sup>).

In parts of East Africa, the rainfall in tsetse-fly infested country exceeds 80 inches *per annum* and in others, such as the dry savannah of Kenya's Northern Province, where *G. longipennis* occurs, the rainfall may drop to 15 inches (381 mm) *per annum*. In East Africa the temperatures vary from maxima of 45°C to minima of 10°C but the range is not as great as it is further south in parts of Central Africa.

In West Africa, Nash & Page (1953) and Page (1959b) studied and described the typical habitats of *G. palpalis* and the effect of climate. In the north, the fly population is confined to the fringing riverine forest, where there is lateral insulation formed by a curtain of creepers and evergreen shrubs, and vertical insulation formed by an interlocking overhead canopy. Small "insulated" feeding-grounds under high shade enable the flies to obtain their food in the dry season without having to venture into the neighbouring savannah with its lethal temperatures.

Sustained high daily maximum temperatures are dangerous, 34°C-35°C being lethal if occurring over ten days. Females appear to be more resistant to such temperature stress; 30% male mortality occurs at 29°C but a comparable degree of female mortality requires an average maximum of 33°C over a period of ten days. In the south, the great difference, due to the more humid and equable conditions, is that *G. palpalis* is not so restricted to a riverine habitat, and can be found at all seasons in small numbers, throughout the savannah woodland, even in the absence of water.

In the north, there is a marked variation in seasonal density. The fly population rises rapidly in the wet season (April-September) and decreases throughout the dry season (October-March). Kernaghan (1962), working about 200 miles (320 km) to the south, has found a similar variation, but Davies (1958) found the reverse taking place (i.e., a dry season peak) 250 miles (400 km) to the south-east. This latter area, with intrusions of the southern rain forest along its rivers, is perhaps more comparable with that described by Page. Here, the fly population tends to remain steady at a low density, except for an increase in the second and third wet months; this is followed by an immediate return to the usual level during the fourth and fifth wet months. The rise occurs when the mean temperature is high and the saturation deficit is falling, averaging 5.5 millibars. This is an optimal figure for rapid reproduction (Nash et al., 1958). By the fourth and fifth wet months, the temperature has dropped, as has the saturation deficit (to an average of 2.7 millibars). A decrease in population can therefore be expected; as in the north, decreases are associated with mean monthly saturation deficits of 2 millibars or less, although this level is not reached until towards the end of the wet season (August-September). This gives a four-month period of increase, compared with only two months in the south. It is considered, therefore, that very high humidity means a reduction in the population of *G. palpalis*, and that the lower densities in the south are due to the shorter duration of conditions favourable or conducive to rapid reproduction.

The average length of life of wild flies is difficult to determine. Nash & Page (1953) give conservative estimates for females of 6-15 weeks and for males of from 4 to 8 weeks, with extreme ages of 6 months and 5 months respectively, attained only by a very small proportion of the population. Both sexes suffer a high "infantile" mortality of 25%.

<sup>1</sup> Data sent to us (1962) for inclusion in this paper.

Of 2490 female *G. palpalis* dissected between January 1958 and October 1959 at Ugbobigha in Southern Nigeria, 46 (2%) were virgin, 764 (31%) had an egg *in utero*, and 221 (9%) a larva *in utero*. The highest pregnancy rates were found in the months with the heaviest rainfall and the lowest mean temperature, saturation deficit and evaporation rate (Jordan, 1962b).

*G. tachinoides* shows a well-marked seasonal variation in density, the chief characteristic being a rapid increase in the early dry season, reaching a maximum about the second or third month, and gradually falling off through the rest of the dry season. This is undoubtedly due in part to the concentration of the fly into favourable habitats as the dry season increases in severity, and as the favourite pupal sites become available on the drying-up of the rivers. During the wet season considerable dispersion takes place, particularly in the third zone, where at this time flies may be found anywhere in the flood plain. In the other zones this dispersion is not quite so obvious, although there are numerous wet-season records of individual flies being caught some considerable distance from their normal location.

The general picture of *G. morsitans* in West Africa is of a seasonal dispersal and concentration. In the wet season, dispersal into the woodland on the higher ground takes place, but as the severe dry-season conditions develop, the fly is forced back into the "forest islands" and thickets of the flood plains. The river bed is not so important to it as it is to *G. tachinoides*, which concentrates here, deserting even the forest islands. Blasdale has made some observations on the climate of the dry season habitat (Glover, 1961b).

Temperature and food supply appear to affect the availability of the females. Warthogs are probably the most important source of food, being common in the flood plains. In the dry season, as the diurnal temperature rises, the flies and the warthogs retreat into the forest islands, so that a food supply is constantly available under the most favourable conditions. The proportion of female flies caught inside the forest islands is much higher than that outside—in one instance, 35% of the total catch inside were females, but only 1% of females were caught outside; more females were obtained if flies were caught while resting on tree trunks (MacLennan & Kirkby, 1958).

In a north-eastern district of Nigeria, in an area where the Sudan and Guinea Savannah Zones merge,

the wet season female population was 9%, which is considered to be the normal proportion. In a very hot season, however, the female proportion was 39%, rising in a breeding-site to 44%. It is considered that this was due to the exceptional heat causing the flies to become very hungry, so that even the females came readily to man (Glover, 1961b). In this connexion, it would be interesting to differentiate between hunger and thirst. Obviously, in this case, water loss (i.e., thirst) would be the most important component, as the high temperature would inhibit activity and consequent energy loss. The prevalence of warthog in *G. morsitans* habitats is largely due to the fact that they are not hunted by the predominantly Moslem local populations.

The seasonal concentration of *G. morsitans* in the Guinea Zones is not so marked as in the Sudan Zone. MacLennan (1958) has pointed out the dry season importance of the "ecotones"—the strips of well-grown vegetation following the upper slopes of drainage lines and standing out from surrounding (usually *Isobерlinia*) woodland. Often the ecotone has the form of rings of taller vegetation surrounding laterite outcrops and open patches of "hardpan" (compacted shallow soil, overlying granite or laterite). In the more southerly parts of the Guinea Zones it has been found that dry season concentration may take place at the headwaters of streams, on the outside edge of the usually well-marked fringing forest. The concentration area may extend for a mile or so downstream (Glover, 1961b).

Page (1959a), working on *G. longipalpis* in Southern Nigeria, close to where the savannah joins the main forest belts, found that in the dry season, when the saturation deficit rose to 7 millibars or more, flies concentrated in patches of forest ("forest islands") which formed the permanent habitat. In the early rains, when the saturation deficit fell to 6 millibars or less, dispersal took place into the savannah woodland. The maximum distance recorded for travel by a fly was nearly 6 km, one fly travelling 2 km in a day. Further north, in more severe conditions, this seasonal movement is likely to be more marked, and may in part account for the apparent discontinuous distribution, as most surveys have been done in the dry season.

In Southern Nigeria *G. tabaniformis* was most plentiful in the middle of the rains and scarcest during the dry season. Estimation of the numbers of *G. tabaniformis* and *G. fusca* combined, during July 1957 and January 1958, suggested that these flies were approximately three times more abundant in the

rains than at any other time. The dry-season decrease in their numbers was thought to have been caused by the adverse effects of high temperatures and low humidities (Jordan, 1962a).

At Ugbobigha in Southern Nigeria, the sex ratio of *G. fusca* was analysed in the wet season and it was shown that the proportion of male flies increased during the day. In the rain forest, 44% of *G. fusca* caught on the fly-round were females; in the riverine forest during the wet season 47% were females, and during the dry season 40%. The sexes emerged from the puparia in equal proportions.

Only 29 specimens of *G. nigrofusca* were caught on an ox fly-round in the rain forest, of which only three were female flies (Jordan, 1962a).

#### *Physiological water balance of tsetse flies*

Studies by Bursell (1959) of the physiological water balance of tsetse flies at rest indicated that there appeared to be no correlation between the fly's resistance to desiccation and its habitat conditions. The rate of water loss of flies in the field was lower compared with flies at rest in the laboratory under the same conditions of mean temperature and humidity, in spite of the fact that the fat consumption of the flies recovered from the field showed that they had been active for some of the time before recapture. These investigations also suggested that flies made use of microclimates of higher humidity than that of the surrounding atmosphere.

#### *Effect of temperature on fat reserves in pupae*

Bursell (1960) demonstrated that at 16°C, when the pupal period of *G. morsitans* was just over three months, some of the smaller puparia would have insufficient fat to complete the development, while at 23°C all but the largest would have used so much fat during development that the teneral fly might have insufficient reserves to enable it to obtain its first meal. Ford<sup>1</sup> observed that in Southern Rhodesia it appeared that cold acting in this manner might limit the range of *G. morsitans* to below an altitude of 4000 feet (1200 m) above sea level in the north of the country and below 3500 feet (1070 m) in the south, as well as in areas covered by soils derived from the Kalahari sands. In such areas it was usual for there to be three winter months with mean temperatures below 16°C. Bursell's hypothesis provided a better fit to the known historical limits of *G. morsitans* for which Jack (1940) had suggested

that the 20°C annual isotherm marked the limit of possible distribution. Similar considerations may apply to the former limits of *G. pallidipes* in Zululand, where field studies (du Toit, 1954) had led to the suggestion that during the winter months emergence of *G. pallidipes* may be prevented by maximum temperatures failing to exceed the threshold of emergence—about 16°C (Jackson, 1946). It would appear likely that the high central plateau of Angola also provides a climatic limit to the southern dispersal of tsetse flies (Sousa Dias, 1952).

Goodier (1958) studying conditions in cleared and uncleared riverine vegetation in Southern Rhodesia, showed that felling trees increased the mean temperature range, which was 27.2°C in cleared as against 22.3°C in uncleared vegetation. On the other hand, the mean minimum temperature in the cleared area was 1.7°C while that in the uncleared area was 4.5°C.

In West Africa low temperatures increase the duration of the pupal period so that the cold season (mid dry season) must result in a lengthening of the life-cycle, and a decrease in the rate of production of adult flies. This is the time when, for other practical considerations, control operations are normally in full swing. In the south, the temperature of the pupal environment is much higher than in the north, and Page (1959b) suggests that this may be connected with the non-infection of *G. palpalis* by *T. gambiense* which is so noticeable in the south.

#### FLY ADVANCES

Fly advances and recessions have no doubt taken place in Africa for a very long time; the most notable recession in recent times being that which followed the great rinderpest epizootic which swept Central and Southern Africa in the 1890s.

Several outbreaks of rinderpest also occurred in Northern Uganda in 1917 and 1926 which greatly reduced the numbers of *G. morsitans* in the areas concerned (Buxton, 1955).

Fuller (1923) expressed the view that the reason for the recession of fly in Southern Rhodesia and South Africa at the beginning of the twentieth century was not the rinderpest alone but also European settlement and the extensive use of firearms for wholesale hunting of game.

It would seem, however, that it is unusual for tsetse flies to be completely exterminated from large tracts of country by agencies such as rinderpest, even when it is coupled with wholesale but unorganized game slaughter. In most instances foci of fly or fly

<sup>1</sup> Data sent to us (1962) for inclusion in this paper.



populations of low density survive which gradually expand back into the country previously occupied (de Sousa, 1960).

Jackson (1933b) described an advance of *G. morsitans* which was taking place in the Kondoa, Mbulu and Singida districts of Tanganyika at the rate of 2-3 miles (3-5 km) per year. From his detailed account of the stages of the advance it was clear that it had not occurred as a result of a mere increase in density of an indigenous tsetse-fly population. He thought that wet years in dry country such as that under consideration might favour the increase of tsetse flies through "suitable 'miombo'" woodland but thicketed or stunted "miombo" was less favourable. Dense, continuous thicket was an absolute barrier where it was wide enough and certain types of thorn woodland, if extensive enough, could delay the advance and might even stop it.

It appeared, though it was not proved, that flies when in small numbers tended to keep to the drainage lines which, under other conditions, were used purely as feeding-grounds. The progress of the advance was thought to depend mainly on the increase of the tsetse-fly population from behind because a larger population would provide a larger number of flies wandering ahead but not because there was any congestion behind. Jackson predicted that the advance was likely to continue southwards and westwards and to join in the west with two other advances from different directions on Singida.

Buxton (1955) mentioned that Swynnerton (1936) reported that the extension westward of the *G. morsitans* advance described by Jackson (1933b) had continued and the fly had crossed the wall of the Rift Valley.

Jackson (1950) described the continuation of this advance, which still went on between Kondoa and Singida and his prediction on the direction in which it would go was on the whole confirmed, but in addition other salients had developed. The fly had penetrated some very dense *Acacia* woodland in the Bubu river valley and its tributary. It had also advanced northwards towards Hanang mountain, leaving the *Brachystegia* ("miombo") woodland and going into savannah-type vegetation with small trees of *Commiphora schimperi* which drop their leaves in the dry season. It was thought that the fact that game, especially wildebeest, was plentiful in this area might be significant.

Swynnerton (1936) had also described an advance of *G. morsitans* which was taking place west of Singida and these two fly-fronts came together in

1939. Buxton (1955) remarked that it was a matter of great interest that, although the flies in the eastern and western areas were both *G. morsitans morsitans*, they differed in colour so that presumably these two groups had been separated for a long time.

In Uganda *G. morsitans* has been known in the Kagera river basin since the early years of the century (Simmons, 1929). By 1930 it had occupied—or at least prevented cattle from using—about 1000 square miles (2600 km<sup>2</sup>) of South Ankole. At this time the fly had reached the Masaka-Mbarara road in the north and extended as far east as the swamps between Lakes Mburo and Nakivali. Between 1931 and 1936 extensive clearings followed up by late fires and the shooting of some buffalo and warthog greatly reduced the fly density and gave rise to hopes that *G. morsitans* would eventually die out throughout the area. This hope was not fulfilled, and by about 1946 the fly was advancing northwards and had apparently occupied all the area between Lakes Mburo and Kachira. A large sheer clearing 1000 yards wide and extending from near Mbarara to Lyantonde had been cut as a barrier to further northward advances of the fly. This barrier failed to halt the advance, either because it was not wide enough or because it was not completed soon enough.

A further attempt to halt the advance of fly by a barrier clearing was made along the Mutonto track and for some years it looked as though the "northern salient" had been contained. In 1948 part of this barrier was sheer-cleared by the Uganda Tsetse Control Department. In 1949 it was discovered that *G. morsitans* was again spreading northwards.

In 1951 the East African Tsetse and Trypanosomiasis Research and Reclamation Organization began a project to eradicate *G. morsitans* from the area by discriminative clearing but *G. morsitans* continued to spread until, by December 1957, it was decided to endeavour to halt the advance with a more drastic clearing programme.

In February 1958, *G. morsitans* was found in small numbers near the Masaka-Ankole border near Kajumbura. This constituted a serious threat to the cattle industry of Masaka, Mubende and Toro and necessitated an immediate change of timing of the clearing, giving rise to grave anxiety, as it appeared that the clearing, which was costing much more and taking much longer than had been anticipated, might fail to prevent further advances. By July 1958, *G. morsitans* had spread to the Lyantonde-Lwenianga road in Masaka.

As a result of this continued advance of fly in 1700 square miles (4400 km<sup>2</sup>) of the Ankole and Masaka districts, the game was shot out to reclaim the area as far south as the Kashongi-Kiruhura road (Uganda, Tsetse Control Department, 1950-60).<sup>1</sup>

Buxton (1955) indicated that clear evidence for *G. pallidipes* advances was available from a few places only. In Zululand, in South Africa, *G. pallidipes* was thought to be confined to three small game reserves, but a great increase took place in the area in which cattle trypanosomiasis was known to occur which was attributed to a corresponding increase in the distribution of this fly.

In Uganda in the late 1930s in the Maruzi area tsetse flies spread towards Lira and reached Aber but subsequently retreated. In the late 1940s *G. morsitans* and *G. pallidipes* started spreading in this area.

Between 1938 and 1942 the Buruli and Bulemezi areas of Uganda were invaded by *G. morsitans* from the north and *G. pallidipes* from the west (Bernacca).<sup>1</sup> Buxton (1955) also mentioned "another important advance of *G. pallidipes* in the districts of Buruli and Bugerere in Uganda", to which attention had been called by Carmichael who had spent many years in Uganda (Carmichael et al., 1948).

In Kenya, unlike Tanganyika and Uganda, very little in the way of fly advances and retreats has taken place, except that there is strong evidence that *G. pallidipes* invaded country around the shores of Lake Victoria after the sleeping-sickness epidemics which occurred at the beginning of the century had necessitated the removal of most of the population and allowed the bush to grow up (Carpenter, 1924, 1926).

Recent surveys on the Suam river in West Suk near the Kenya-Uganda border, however, have revealed that an advance of *G. pallidipes* which may still be in progress appeared to have taken place up the Turkwell river and the Suam (Fairclough, 1961).

*G. swynnertoni*, which inhabits a large part of Northern Tanganyika, extends into a small section of south-western Masailand in Kenya. Lewis (1934) thought that this fly had recently invaded Kenya. Later, Lewis (1942b) found that it was making rapid advances. Now, however, *G. swynnertoni* appears to have reached the limit of its habitat and altitude range in Kenya. Buxton (1955) referred to a recent advance of *G. swynnertoni* at a point near Lake Eyasi in Tanganyika.

De Sousa (1960) in describing the advance of *Glossina* in southern Mozambique, said that this great tsetse-fly advance had been observed first in Mozambique and later in Southern Rhodesia. It involved *G. morsitans* and *G. pallidipes* and extended over a very large front across Portuguese territory from the coast to the Lundi drainage basin in Southern Rhodesia. The rate of progress of the advance, although variable along the whole front, according to local conditions, seemed to be greatest in the west and south-west. The general direction of progress was towards the south-west along the Lundi drainage system with the river as its axis.

Although the advance southwards in Mozambique might be checked by a very dry zone which lay across its path, movement to the southwest and south in Rhodesian territory might find favourable conditions for progress through country where intensive settlement of people was not practical.

In the present advance the fly seemed to be re-occupying the areas it had held before the rinderpest epizootic of 1896. The areas in danger of reoccupation by the tsetse fly included the low veld of Southern Rhodesia, extensive parts of the Northern Transvaal, all of the Kruger National Park and a large part of the Limpopo valley in Mozambique.

Ford (1960) described the same advance of *G. morsitans* and *G. pallidipes* followed by *G. austeni*, which had been in progress for many years, starting in Mozambique, and from 1942 continuing in Southern Rhodesia. He also considered that this fly advance was a movement towards restoring the fly situation which had prevailed before the great rinderpest epizootic had swept over Southern Africa, because it threatened to engulf the south-eastern low veld of Southern Rhodesia as well as large areas of the Northern Transvaal. The main direction of the advance was likely to be to the west and south but an arid zone in Mozambique between the Rio Save and the Limpopo river might prevent movement of the fly due south in Portuguese territory.

The speed of this fly advance had been influenced by the nature of the country over which it had swept. Although the country now threatened contained extensive areas of grassland and sparse woodland, these could be by-passed where riverine forest and woodland provided suitable corridors. In the high country there were favourable habitats for the fly in the *Brachystegia* woodland. The country was not as a whole suitable for dense settle-

<sup>1</sup> Data sent to us (1962) by J. P. Bernacca for inclusion in this paper.

ment but there were places where settlement might provide barriers to local fly advances.

This advance has created an international problem and is the biggest threat of increased tsetse-fly infestation existing anywhere in Africa.

In Northern Nigeria advances of *G. morsitans* in the Guinea Zone have been recorded in the past ten years. From 1952 onwards, large tracts of country, hitherto free from *G. morsitans*, have been invaded. In 1958 Wilson described an advance on the north-eastern edge of Belt 27 in the Pambeguwa-Kudaru area, which was first detected by Nash in 1944. In spite of the creation of barrier clearings, the use of insecticides and other control measures to check this advance, by 1955 *G. morsitans* had spread right across the widest part of the Anchau fly-free corridor until, in April 1958, the Kano river was crossed to the east of the Ririwai hills. The fly is probably still advancing.

In 1955 Davies recorded a tsetse-fly advance which had taken place in the Song region of Adamawa between 1930 and 1955 and Wilson, in 1958, also described an advance of *G. morsitans* in the Doka-Shika areas. He also mentioned an advance in the Kontagora area. In 1959 Tarry discovered that *G. morsitans* had moved 20 miles (32 km) south on a 30-mile (48-km) front since Belt 27 was first shown on the veterinary tsetse and trypanosomiasis map (Glover, 1961b).

The movement of *G. palpalis* within the linear riverine habitat characteristic of the northern areas of Nigeria has been studied by Nash & Page (1953). Travel (i.e., movement of individuals over a distance of more than 900 m from the point of marking) is maximal at the end of the wet season and minimal at the end of the dry season and in the early rains, the hottest time of the year. Temperature rather than humidity therefore seems the most important factor. The longest distance of travel recorded was 5 km, but it is doubted whether *G. palpalis* often travels more than about 3 km from its place of emergence during its lifetime. In the south there is a tendency for the fly population to be less static than in the north. In a wet season experiment, only 0.36% of the flies released at a point were recaptured at the same point, after 18 days, in the south. In the north 3.8% were recaptured after a similar interval. In the dry season the figures were 0.81% and 7.52% respectively (Page & McDonald, 1959). Long distance travel may of course be encouraged by climatic conditions permitting the fly to make unobstructed flights along the outer edge of the

fringing forest, or by an uninterrupted river bed, i.e., one free from low vegetation which might obstruct the flight line. On wide watercourses such as the Niger and Benue rivers, flies may travel considerable distances over the water.

There are unfortunately very few data on the extent to which cross-country movement takes place. Nash & Page (1953) record two instances of single flies crossing a watershed, one having traversed at least a mile of woodland. On another occasion, again in the north, near the same locality, several flies crossed a watershed of two miles, but had undoubtedly followed people along a well-used footpath (Kernaghan—unpublished data).

#### RESTING-SITES

##### *Negative reaction to light*

The work by Pilson & Leggate<sup>1</sup> recalls the experiments of Jack & Williams (1937), which demonstrated that *G. morsitans* entered the darkened portion of an appropriately designed apparatus when the temperature was 30°F (−1°C). Such behaviour, or “negative reaction to light” might indicate the mechanisms which caused flies to avoid high temperatures. Various workers in different parts of Africa—Potts (1933) and Nash (1935)—have shown that *Glossina* cannot live long at 40°C and this fact is important because in the Zambezi valley daily maximum temperatures of over 40°C are commonly observed (Ford<sup>2</sup>).

##### *G. swynnertoni*

Southon (1958) made observations on *G. swynnertoni* marked with small, reflecting, glass spheres compared with unmarked flies located at night in thornbush at Shinyanga in Tanganyika. Both marked and unmarked flies moved at dusk from the normal diurnal resting-sites on the undersides of branches to the upper surfaces of leaves and returned to the branch resting-sites at dawn. These observations confirm and extend those made by other workers (Jewell, 1956, 1958; Rennison, Lumsden & Webb, 1958).

Also at Shinyanga in Tanganyika, it was found that in the short, wet season *G. swynnertoni* rested on the undersides of branches of small trees in hardpan areas. Samples of flies found in resting-

<sup>1</sup> Pilson, R. D. & Leggate, B. M. *A diurnal and seasonal study of the resting behaviour of Glossina pallidipes Austen* (to be published).

<sup>2</sup> Data sent to us (1962) for inclusion in this paper.

sites had a different composition from those taken on fly-rounds, mainly in showing a higher percentage of females and engorged male flies (Isherwood, 1957).

In the Mara area of Masailand in south-western Kenya, *G. swynnertoni* rested on the shady sides of the trunks and undersides of branches of trees and shrubs. It appeared to favour resting on some species of plants more than on others and it was discovered that the size and shape of the plants chosen by this fly as resting-sites were important factors (Langridge, 1960a).

#### *G. morsitans*

In Nyasaland, Lamborn (1916) found *G. morsitans* resting on the larger trees, especially baobabs, and Buxton (1955) remarked that the suggestion that female flies could be found in greater proportions in such places had been confirmed and it had been shown that occasionally the females may even exceed the males. Female flies could be seen "deep in the recesses between the buttresses and component parts of the trunk, and in the hollows and fissures of the bark of the older trees, and they often occur high up and out of reach", but the males seemed to rest as a rule in more obvious positions.

Blasdale records temperatures on the trunk of a tamarind tree and in its crevices (Glover, 1961b). At ground level, temperatures up to 10°C lower than the air temperature (40°C) were noted. At a height of 1.25 m, the maximum difference, found in a crevice, was almost 6°C, except in a hole 15 cm deep, where the temperature was 10°C lower. This evidence supports the view that tree-trunks (as opposed to leaved and small branches) usually within the forest islands, are the important dry-season resting-sites of *G. morsitans*. MacLennan & Kirkby (1958) found *G. morsitans* resting up to 2 m above the ground, although Davies & Blasdale (1960) found that in the hottest part of the day very few flies rested above 1.25 m. Blasdale noted that temperature affects activity, air temperatures higher than 39°C rendering the flies inactive (Glover, 1961b).

In the Guinea Zone resting-places of *G. morsitans* have been fairly well observed. Nash (1952) found that the majority of gorged flies rested head upwards on tree-trunks and branches over 1 m above the ground, and then, after the exudation of liquid that occurs after gorging, moved upwards to a height of 2-4.3 m, and took up a position head downwards, so that they had a much wider field of vision. Some flies, however, took up a horizontal position, dorsum downwards on the underside of branches. This has

been confirmed more recently by Aitchison (Glover, 1961b), who found flies resting on the underside of branches 2-4 m above the ground in *Isoberlinia* woodland. The branches were usually stout and free from smaller branches or leaves. The 3-m level appeared to be most popular, with the head pointing away from the trunk. The bark was dark-coloured and rugose, no flies ever being seen on smooth, light-coloured branches. Although most flies were found on *Isoberlinia doka*, this is not considered significant, as it happened to be the commonest tree. Other species on which flies were found included *Lannea schimperi*, *Cussonia nigerica*, and *Butyrospermum parkii*.

Elsewhere, Buxton (1955) said that Jackson had told him that male *G. morsitans* and *G. swynnertoni* rested under overhanging branches up to 12 feet (3.6 m) from the ground.

#### *G. longipennis*

Langridge (1960a), working in Kenya, studied the resting-sites of five species of tsetse flies and found that log sites and the shady side of tree-trunks and the undersides of branches of multi-stemmed trees with easy access to game paths were essential to *G. longipennis* in the dry savannah country of Central Kenya.

#### *G. brevipalpis*

In the same area, when the vegetation was in full leaf, *G. brevipalpis* dispersed from its normal habitat in tall thicket on lava flows into the more open country normally associated with *G. longipennis*, but it did not range far. In the coastal forest *G. brevipalpis* rested in the dry weather in places where the evergreen vegetation in the lower canopy was more shady than in the semi-deciduous surroundings. It was frequently found perching on thin, looped-over and horizontal branches up to three feet (90 cm) from the ground near game paths.

#### *G. pallidipes*

This fly was found in a wide range of habitats in different parts of the country. In the dry season in the coastal forest it used similar resting-sites to *G. brevipalpis* and in the dry savannah country of Central Kenya it was often found in sites used by *G. longipennis*.

Isherwood & Duffy (1959) studied the resting habits of *G. pallidipes* on two transects across the Ruma thicket in the Lambwe Valley of Kenya. The first transect consisted of a series of contiguous 100-foot (30-m) squares and the second consisted

of 100-foot  $\times$  50-foot (30 $\times$ 15-m) squares separated by 100-foot intervals. Searches for resting flies were made every five minutes by four trained Africans. The first transect was searched during five periods between 17 May 1957 and 26 February 1958, and the second transect was searched in two parts, the first between 6 and 24 January 1958 and the second between 3 and 14 March 1958. Sectors in the two transects were grouped together according to the vegetation types in which they occurred. These were:

- (1) Forest dominated by *Euphorbia candelabrum*,
- (2) Continuous thicket,
- (3) Thicket clumps separated by wooded grass-land.

Striking changes in the distribution of resting flies were observed. In the first period numbers of resting flies were found in the thicket clumps on the eastern edge of Ruma; subsequently large numbers were found in the contiguous thicket; and eventually the greatest numbers were found in the forest. The general picture of fly distribution within the vegetation phases in the transects agreed with fly-round observations but was quite different from trap catches.

The gross changes in distribution of the fly were accompanied by changes in composition and size of the active and resting catches and in changes in the relations of the catches to each other. Female resting flies were always more numerous but the ratio changed markedly, from 1.5 to 1.23. The opposite was true of males, the ratio varying from 3 to 16. Active male flies were more numerous than resting ones whereas the reverse was the case for female flies. This peak in active male fly catches corresponded with least hunger in the resting male population.

During the first three searching periods on the first transect, engorged male flies were less numerous than engorged female flies, but the situation was reversed during the last four periods though no explanation was given for this observation.

It was hoped that the work on the transects would help to elucidate the application of the feeding-ground theory to *G. pallidipes* but the results were conflicting.

There was no clear-cut correlation between the distribution of the flies and temperature variations, but the authors thought it possible that the change in distribution of the flies was the result of changes in the distribution of the host animals.

Pilson & Leggate<sup>1</sup> demonstrated that during most of the year *G. pallidipes* in the Zambezi valley in Southern Rhodesia rested on branches of trees and shrubs in riverine vegetation, at heights of generally over three feet (90 cm) above the ground. In hot weather, however, such sites were used only in the early morning and towards sunset. When the air temperature rose above 30°C there was a movement of the flies to sites on the boles of trees below three feet from the ground, to fallen logs and to rot-holes in large trees.

#### *G. austeni*

Langridge (1956) showed that *G. austeni* was confined to the forests and tall thickets of the coastal belt. In the hot dry weather it could be found perched on the undersides of horizontal branches up to three feet (90 cm) from the ground, in the dense undergrowth of the forest which provided the deepest shade.

#### *G. fuscipleuris*

Isherwood (1958), while visiting the Mitoma country of Ankole in Uganda, on two occasions found *G. fuscipleuris* in riverine vegetation resting on the undersides of leaves or the vertical surfaces of branches of shrubs "which grew in an arch-like arrangement". Resting flies were difficult to catch and, once disturbed, were rarely seen again.

#### *G. palpalis*

Little is known of the resting-sites of *G. palpalis*. Resting flies (as distinct from hunting flies, which may often be seen alighting on the ground or on vegetation close to the observer) are extremely elusive. They have, however, been observed on twigs or leaf petioles about 1 m above the ground, and to remain motionless for several hours. When disturbed they have been known to return immediately to exactly the same spot (Kernaghan—unpublished data). McDonald (1960a, 1960b), using fluorescent paint as a marking agent with subsequent detection by ultraviolet light, has investigated the night-time resting-sites. He has found that, if flies are liberated, more than half rest during the night within 30 cm of the ground on leaves and small twigs, but never on tree-trunks or branches. Most of the remainder have been found at about 1 m from the ground, with very few as high as 2 m.

<sup>1</sup> Pilson, R. D. & Leggate, B. M. *A diurnal and seasonal study of the resting behaviour of Glossina pallidipes Austen* (to be published).

*G. tachinoides*

In studying the resting-sites of *G. tachinoides*, Moiser (1912) recorded that six men posted in trees for an hour at heights ranging from 10 to 25 feet (3-7.6 m) never saw a fly, whereas observers on the ground found flies at rest on the underside of small branches generally within a foot of the ground and most frequently at about 6 inches (15 cm). In a further experiment he confirmed these observations and found that this fly rested close to the ground in an inverted position on the undersides of horizontal twigs. More recent work with flies marked with fluorescent paint has shown them to have a tendency to rest head upwards, more often on stems than on leaves, about 3-4 feet (0.9-1.2 m) from the ground, with occasional ones somewhat higher. This was, of course, at night (Glover, 1961b).

## FEEDING HABITS

*Attractants*

Fiske (1920), studying the feeding habits and host animals of *G. fuscipes* on Lake Victoria, noted swarms of flies following and biting *Varanus* lizards, situtunga, crocodiles, tortoises and domestic pigs running wild on the islands.

Duke (1933), visiting an area in the north of Uganda in 1932, observed *G. brevipalpis* attacking man after almost all the animals had disappeared as a result of a rinderpest epizootic and after hippopotamus had finally been driven away.

Swynnerton (1936) thought that bushpig was an important food for *G. pallidipes*, *G. austeni* and *G. brevipalpis*, and that these flies much preferred donkey and cattle to man, but man to sheep or goat.

Jack (1941), in the south-eastern part of Southern Rhodesia, collected large numbers of *G. pallidipes* from screens and traps but noted that very few of these flies appeared to visit a motor car (Buxton, 1955).

Vanderplank (1944) studied the attractiveness of a number of different animals and baits for *G. pallidipes* and found that dog, ox and porcupine were the most attractive; domestic pig was also attractive but bushpig was not tested; next came sheep, goat, man and baboon and, finally, serval cat, lion and jackal.

Chorley (1948) demonstrated that *G. pallidipes* was attracted by the scent of cattle dung and urine, and many field workers have observed that tsetse flies appeared to be attracted by the smell of the dung and urine of elephant and buffalo.

Johns (1950), working in Zanzibar, found that test catches of *G. austeni* with oxen were considerably greater than with screens, even when attempts were made to impregnate the screens with ox scent.

By means of his "animal" traps, Morris (1960a) showed that *G. pallidipes* followed herds of elephant passing through fly-infested country in the Busoga district of Uganda.

Hughes (1957) examined the responses of *G. morsitans* to a selection of aliphatic acids, alcohols, esters and amines. Exhaust gases and distillates of sump oil were also tested on the activity of *G. palpalis*. The results obtained were consistent with those of other workers, in that it was found that stimulating compounds might be present in very small quantities in sump oil.

Johns (1959), working in the laboratory at Shinyanga, studied the olfaction of *Glossina*. Three olfactometers were tried but no satisfactory response was observed when tests were made with *G. morsitans*. Odours from anhydrous lanoline and warthog extract in alcohol or water were tried without success, though these are known to be attractive to flies in the field (Langridge, 1960a).

Langridge (1960b), working in Kenya, also showed that *G. pallidipes* could be attracted to fly-rounds by using bait attractants prepared from sheep wool greases and extracts from pig hair- and skin-scrapings. Further field experiments (Langridge, 1961) revealed that traps treated with attractant were more effective in catching *G. pallidipes* and *G. fuscipes* than fly-boys. These treated traps quickly revealed the presence of flies where ordinary catching methods failed to do so.

Barass (1960), of the University of Rhodesia and Nyasaland, found that tsetse flies preferred to settle on the sunny side of screens rather than on the shady side. The attractiveness of a striped black and white screen was progressively reduced as the width of the white stripes was increased. Even a screen with narrow white stripes was less attractive than a completely black control screen. The effect of the breaking up of the black screen did not diminish the attraction for the fly to the black screen.

*Identification of blood meals*

Early work on the identification of the natural hosts of tsetse flies by serological methods was carried out by Symes & McMahon (1937), but Weitz (1952) devised a really reliable precipitin test involving the inhibition of agglutination of tanned red cells. Later, a more specific test was carried out

by Weitz & Jackson (1955) at Daga Iloi in Tanganyika. Since then this new technique has been further developed and identification of natural hosts of many tsetse species has been made possible.<sup>1</sup>

#### BREEDING-SITES

##### *G. swynnertoni*

Burt (1952) studied the breeding habits of *G. swynnertoni* near Shinyanga in Tanganyika and found pupae in large numbers during the dry season but very few in the wet season. Newly emerged flies were found during the wet season and adult tsetse flies were abundant, so that it could not be supposed that there was a cessation of breeding at this time.

After several years of investigation, it became apparent that female flies, when about to deposit larvae, often perched on the undersides of logs or branches raised a little above the ground. The importance of these particular perches on the underside of logs was demonstrated by the fact that females returned to them after long periods of time. During the wet season pupae might be found on the surface of the soil, protected by dense overhead cover.

Female flies placed in cages with trays of damp soil produced larvae which were unable to penetrate into the soil and often pupated on the surface, where they were difficult to see owing to the particles of mud adhering to them. During the dry season pupae were buried in the looser soil, doubtless because the larvae could penetrate it more easily. There was also a change of breeding-places at different seasons, pupae often being found in thickets beside rivers during the hot dry season, but not in the early part of the dry season.

In south-western Masailand in Kenya, the breeding-sites of *G. swynnertoni* are mainly under logs and trees broken or pulled down by elephants in fairly open savannah country, preferably on and around stony hillsides.

##### *G. morsitans*

Harley (1954) studied the breeding-sites of *G. morsitans* in the Singida and Kahama districts of Tanganyika. In the *Brachystegia* woodland of Singida, pupae were found under logs at all three seasons when the searching was done. No pupae were found under logs less than 2½ inches (6.3 cm) in diameter. Pupae were more scattered in the rainy

season. The average number of pupae per log site was 5.2 in June, 5.0 in October in the dry season and 2.1 in April during the rains. In Kahama, in country similar to that in Singida, pupae were found in the same kind of sites but in smaller numbers.

Glasgow (1961a), studying *G. morsitans* in Central Tanganyika, found that log sites were the most productive breeding-places during the rains and early dry season; thereafter rot-holes in trees became temporarily the most productive sites; in general, burrows in the ground and rock sites were not important. These records were made over five years, from 1956 to 1960.

In Northern Nigeria, Lloyd et al. (1924) recorded that the breeding of *G. morsitans* and *G. tachinoides* appeared to be confined mainly to the dry season, but Nash (1937, 1939) showed that in the Sudan Zone *G. morsitans* bred throughout the wet season except in August. Nash (1939) classified the different breeding-sites of *G. morsitans* in the Sudan Zone into "residual forest islands", "small thickets", "margins of the river beds", "logs and fallen trees" and "seedling palms" (Glover, 1961b).

##### *G. pallidipes*

Parsons (1954) made observations on a breeding-place of *G. pallidipes* in evergreen shrubs on the Kiangini river in the Makueni area of Kenya, by means of hand searching for pupae over a period of about five years. The results were correlated with records of the adult fly population, rainfall and temperature.

Searches were made in three areas, each covering 200 square yards (167 m<sup>2</sup>) and divided into 50 small squares. Two of these areas were searched monthly and the third once every three months. The numbers of live puparia found varied widely with the seasons and only a few could be discovered in the rains. The greatest numbers occurred during the hottest, driest periods. The hatching time of the pupae collected at different times varied between 35 and 40 days and the sex ratio of the emergent flies was approximately equal. The proportion of puparia parasitized by *Thyridanthrax* sp. at different times varied between 5% and 77%.

##### *G. longipennis*

Lewis (1942a), working in Kenya, stated that the sites which seemed most favourable for larviposition by *G. longipennis* were logs, leaning tree-trunks and the stumps of felled trees near shrubby or woody thickets. *G. longipennis* puparia could also be found

<sup>1</sup> See the article by B. Weitz on page 711 of this issue.

under logs in open country hundreds of yards away from dense bush and in the shade of a single tree in the savannah.

Langridge (1959) noted that *G. longipennis* used the thicket on lava flows near Kiboko in Kenya in the wet season in preference to the more open log sites which it used in the dry season. Also in this area *G. brevipalpis* used the same kind of sites in the thicket on the lava flows in the wet season.

#### *G. brevipalpis*

In the dry season in dry savannah country *G. brevipalpis* used riverine vegetation, preferring patches of dense low-growing shrubs such as *Salvadora persica* and *Craibia* sp., usually in the dense shade towards the middle of the clumps, whereas *G. pallidipes* appeared to prefer the outer edges of the clumps.

In the coastal forest *G. brevipalpis* could be found almost anywhere in the loose earth on the forest floor.

#### *G. fuscipleuris*

Isherwood (1958) found very few full puparia of *G. fuscipleuris* at Mitoma in Ankole in Uganda but empty shells were fairly abundant. Puparia and shells were found mainly at the bases of trees, and particularly productive sites were found where several small trees were grouped together. Puparia were also found under low thicket at the base of a termite mound and in one place under recumbent trees. Most of the full puparia and shells were found towards the edges of the riverside vegetation.

#### *G. austeni*

Johns (1950), searching for the pupae of *G. austeni* on the island of Zanzibar, found that there this fly showed a preference for sites under walls of coral rock. Only a very few pupae were found under dead trees.

Langridge (1956), working in the Sokoke forest near Kilifi on the Kenya coast, searched for pupae of *G. austeni* in *Afzelia* and *Manilkara* forest, which is very dense and which occurs on red sandy soil. He also searched in *Brachystegia* forest, which is more open and grows on light, sandy, grey soil in places lower down, and in the not always clearly defined inter-zone between these two main forest types.

Most *G. austeni* pupae were found in the densest parts of the *Afzelia-Manilkara* zone in places where the light in the undergrowth was less than 10% as strong as that outside in the open.

#### *G. fuscipes*

A fair amount of work was done on the breeding-sites of *G. fuscipes fuscipes* on the shores of Lake Victoria in the early part of the century (Carpenter, 1912, 1913, 1919, 1920, 1923; Fiske, 1913, 1920; Duke, 1919) and later by Chorley (1944), but since then little about this subject can be found in the literature.

However, from our own experience of this fly, its main requirements for breeding-sites are those described by Buxton (1955), quoting Fiske (1920), who emphasized that a breeding-place must be shaded by something reaching to within two or three feet (about 1 m) of the ground, but that the shade provided by tall trees without low branches is not suitable. The shade in a breeding-site may be provided by low branches of trees or shrubs or even herbs and even by such objects as rocks or stumps of trees. Breeding may also occur in shallow caves with sandy floors.

Buxton (1955) went on to say that most of the known breeding-places of *G. fuscipes* were dry, sandy or gravelly beaches close to the shore of the lake.

Fiske (1920) noted a distinct type of breeding-site among fine, dry, vegetable debris. He found suitable deposits of material under rocks or lying on top of them or on coarse ground and pebbles; but, to be suitable for the breeding of *G. fuscipes*, the material had to be either sheltered from the sun or well drained; if it was saturated it was not attractive.

#### *G. palpalis*

The wet-season breeding-sites of *G. palpalis* in Nigeria have not yet been established. Pregnancy dissections show that breeding does not cease and while it is assumed that breeding must take place on ground free from inundation, possibly at the edge of the savannah woodland, extensive research has failed to produce any evidence. In the south, even in the dry season, pupae are difficult to find, owing to the extensiveness of the possible breeding-sites. The pregnancy dissections showed that whereas in the north 75% of the females were pregnant, in the south the figure was only 31%, possibly another reason for the low population level usually found in Southern Nigeria. Jordan (1960a) notes that the figures for those flies with an egg *in utero* are comparable in both regions, and suggests that in the forest belt there is some adverse factor which causes abortion in the early stages.



*G. tachinoides*

Wet-season breeding-sites have still not been found, and it is not yet known whether there is a complete cessation of breeding in the heavy rains. Kernaghan (unpublished data) carried out an investigation in which the banks of a stream, the bed of which was a prolific dry-season breeding-ground, were methodically searched throughout a wet season. Once the river bed became too wet, no more pupae were found at all, although the continued maintenance of the adult fly population indicated that breeding must have been carrying on.

*G. longipalpis*

*G. longipalpis* breeding-sites, typically under logs in the forest, have been observed only in the dry season. It is not known whether breeding ceases during the heavy rains. This is in contradiction to Morris (1934), who states that no breeding takes place in the dry season.

*The fusca group*

Jordan (1962b) made extensive searches in "Lowland Rain Forest" in Southern Nigeria for puparia of *G. tabaniformis*, *G. fusca* and *G. nigrofusca*. Particular attention was paid to "classical" tsetse-fly breeding-places such as under logs or overhanging banks of streams and in the shelter of tree roots and buttresses, but very few puparia were found. Occasional puparia were found in the litter on the forest floor, and it is possible that the larvae of these species are not deposited in any special site.

## PREDATORS AND PARASITES OF TSETSE FLIES

In Northern Nigeria experiments were carried out by Taylor (1932) on the natural parasitism among pupae of *G. tachinoides* and *G. morsitans*. It was found that the rates of parasitism were low compared with those in Southern Rhodesia (Chorley, 1929). Experiments were also carried out by Lloyd et al. (1927) with some *Syntomosphyrum glossinae* Waterst. on *G. morsitans* and *G. tachinoides* pupae, but they appeared to have failed. However, in 1947, Nash found that his stock of laboratory *G. palpalis* puparia had become heavily parasitized by *S. glossinae*. This was the first record of *Syntomosphyrum* being found in wild puparia in Northern Nigeria.

In East Africa Glasgow (1953) studied the possibilities of the "extermination of animal populations by artificial predation and the estimation of populations" and defined artificial predation as a "pre-

dator-prey relationship in which the predator is man". In an experiment in which a population of tsetse flies was subjected to artificial predation the "geometrical expectation was fulfilled closely", confirming the theoretical demonstration of the fact that the reduction of a prey population by means of artificial predation could be expected to follow a geometrical progression. "By summing the geometric series", Glasgow showed that in this experiment it was "possible to estimate the initial prey population and birth rate of tsetse". His estimates coincided closely with independent estimates made by releasing and recapturing marked flies before artificial predation was begun. The element of immigration, which was included in the assessment of the birth-rate in both methods of estimation, had a low numerical value which, although negligible when the population was large at the beginning of the experiment, proved big enough to prevent ultimate extermination of the fly by artificial predation.

Southon (1959) investigated the predatory fauna of rot-hole breeding-sites of *G. swynnertoni* in Tanganyika. In discussing pupal predation, he mentions Whiteside's (1951) suggestion that a large proportion of pupae were taken by ants such as *Pheidole* and ponerine ants; the latter were found in rot-holes in trees which were suitable potential breeding-sites for the fly but contained no tsetse pupae.

Southon also studied predation on *G. swynnertoni* in the early phases of emergence of the fly from the pupa, before the initial flight and in the active phases when the adult fly was predominantly in flight. Most previous records of predation refer to the adult non-teneral fly. These records include birds, dragonflies, robber flies (Asilidae), bembecid wasps and spiders (*Nephele*). Three hundred and thirty Asilidae were caught by Southon with prey, 15% of which was *G. swynnertoni*.

The fauna of trees on which *G. swynnertoni* rested included numerous predators of the families Mantidae and Reduviidae as well as spiders, ants and beetles. The study of the feeding habits of some of these predators made the direct estimation of predation from field observations possible, particularly for a spider, *Hersilia setifrons*, found on trunks and branches of most trees.

In collaboration with Dr B. Weitz, an attempt was made to develop a serological method by which specific proteins of *Glossina* might be identified in the stomach contents of predators.

Saunders,<sup>1</sup> working at the London School of Hygiene and Tropical Medicine, kept records of the parasites which emerged from pupae sent to him from Central Kenya. In eight batches of *G. pallidipes* dispatched between July and October the proportion of parasitization by *Thyridanthrax* (possibly three species) varied between 6.1% and 16.2%. The emergences of this parasite from *G. brevipalpis* and *G. longipennis* puparia were based on much smaller numbers and the percentages parasitized were therefore more variable.

Six *Stomatocera* were obtained; one from a *G. pallidipes* puparium from Makueni and five from *G. pallidipes* puparia from Kiboko, giving a percentage parasitization of 1.44, but the total percentage of this species which emerged from 3530 *G. pallidipes* puparia was 0.17.

Four puparia of *G. pallidipes* from both Makueni and Kiboko were parasitized by *Syntomosphyrum*, giving a total percentage parasitization for this insect of 0.11.

#### EPIDEMIOLOGY

The epidemiology of human trypanosomiasis in Africa, and particularly West Africa, is reviewed elsewhere in this issue by Willett.<sup>2</sup> A detailed account of the epidemiology of sleeping-sickness in East Africa has also been given by Morris (1959, 1960b, 1960c, 1960d).

Ashcroft (1959), in Tanganyika, considered recent work on the identification of animals on which tsetse flies fed in relation to previous investigations on the incidence of trypanosomiasis found in these hosts and their susceptibility to experimental infection with trypanosomes. He reached the conclusion that some animals, such as warthog, may be less important as reservoirs of trypanosomiasis than might be expected from their importance as hosts of tsetse flies, whereas other animals, such as kudu, giraffe and reedbuck might be more important. He suggested also that the number of tsetse flies carrying trypanosomes and the relative proportion of the different species of trypanosome occurring in an area might be closely related to the host animals on which the tsetse flies fed.

Ford & Leggate (1961) showed that in Southern Rhodesia trypanosome infection rates in *Glossina* varied in relation to geography and climate and

demonstrated a positive correlation between infection rates and the distance from the middle of a *Glossina* belt at the latitude of 7°S. They thought it probable that this was the effect of the decrease in mean annual temperature, corresponding to the increase in distance from the equator. They also found that the pathogenic trypanosomes infecting cattle were *T. congolense* (65%), *T. vivax* (20%) and *T. brucei* (2%). Some 13% of infections were mixed; but these were only approximate percentages, as there appeared to be a wide variation in infection rates from year to year. Since the widespread use of quinapyramine (Antrycide), *T. vivax* had formed a much higher percentage of infections.

There was, so far, no detailed classification of the *T. congolense* and *T. vivax* groups, but this investigation showed that *T. dimorphon*, and probably *T. uniforme* also, were recognizable. Infections in sheep and goats were caused by *T. congolense* and *T. brucei*, in horses, donkeys and dogs by *T. congolense* and *T. vivax* and in pigs by *T. suis* or *T. simiae*.

W. S. Steele<sup>3</sup> states that *T. rhodesiense* is endemic in some areas of Rhodesia but seldom reaches significant proportions.

#### ACTIVITY

##### *G. austeni*

Johns (1950), studying populations of *G. austeni* on Zanzibar, observed that standing catches over periods of 6 and 11 hours showed an increase in activity of this fly in the morning and afternoon, but they were still quite active at mid-day.

##### *G. pallidipes*

Buxton (1955) noted that Vanderplank (1941), using a bait ox for about 11 months in Tanganyika, found that he caught much larger numbers of *G. pallidipes* on days following dark nights than on those which followed moonlight nights.

Later Vanderplank (1948) showed that *G. pallidipes* could find a man and bite him in a room lit only by starlight coming through the window. If the room was blacked out, biting was rarer.

Chorley & Hopkins (1942) carried out fly-rounds at night with a bait ox in the Buruli district of Uganda. On a moonlight night, working from sunset to sunrise, they caught nearly 50 *G. pallidipes* but later in the same month on a moonless night they caught only about half a dozen flies although

<sup>1</sup> Personal communication (1957) to the Chief Zoologist, Department of Veterinary Services, Kenya.

<sup>2</sup> See the article on page 645 of this issue.

<sup>3</sup> Data sent to us (1962) for inclusion in this paper.

there was some evidence of activity all through the night even when it was very dark (Buxton, 1955).

Pilson & Leggate (1960) in Southern Rhodesia studied the diurnal activity of *G. pallidipes* which were allowed to engorge on tethered oxen throughout the period of activity, i.e., between 04.45 and 19.00 hours each day. In hot dry seasons there was a slight peak in feeding activity in the early forenoon, followed by steady feeding during the day. From noon onwards the feeding activity increased rapidly and ceased abruptly between 18.45 and 19.00 hours. During wet seasons, fewer flies attacked the animals and there was no morning peak; instead, there was a gradual rise in feeding activity until the late afternoon, followed by a fall-off and cessation between 18.45 and 19.00 hours.

#### *G. longipennis*

Field experiments in Kenya by Power (unpublished data, 1962) confirmed that *G. longipennis* was hardly active to man during the daytime, but exhibited a burst of activity starting just before sunset. It seemed likely that this was triggered off by a steep and sudden decline in light intensity. The catch started to rise about 10 minutes before sunset and reached a high level which was proportional to the saturation deficit; a higher catch was obtained under drier conditions. A much smaller burst of activity occurred at dawn, beginning at the same light intensity as that at which the evening activity started; a lower temperature was thought to account for the much smaller numbers at dawn. As a result of this work, it was suggested that patrols to discover the presence of *G. longipennis* should be confined to a one-hour period, starting an hour before sunset. Such catches would reveal the presence of fly which might not be detected by daytime patrols (abstracted by E. F. Whiteside).

#### *G. morsitans orientalis*

Welch (1958) studied the intensity of the activity of *G. morsitans orientalis* at different times of the day in Tanganyika. This fly was taken at all times of day on experimental fly-rounds, but less often before sunrise and after sunset. He also found some indication of a very slight diurnal cycle with two peaks of activity, one in the morning and one in the afternoon, but this was frequently overshadowed by other factors. Reductions in temperature and saturation deficit, usually caused by an increase in cloud cover, by rain, or by both, led to intensified activity of the fly.

Harley (1960) studied the "range of dispersal of *G. morsitans*" at Ankole in Uganda, from release points which were considered to be surrounded by a hypothetical series of concentric circles with radii of 500, 1000, 1250, 1500, and in some instances 15 000 yards (or about 450 m, 910 m, 1140 m, 1370 m and 13 710 m).

From his results it appeared that few of the flies recaptured had moved further than 6000 yards (about 5490 m) from the point of release and probably 90% were caught within 3000 yards (2740 m) of it. It was subsequently realized, however, that these results applied only to the flight range of *G. morsitans* rather than showing true dispersal. Nevertheless they were of interest in that they denoted the chances of tsetse flies reaching one area from another of similar size at a given distance, which was important when the possibilities were being considered of flies invading one area from another or causing outbreaks of trypanosomiasis at varying distances from the known edge of a fly-belt.

#### *G. morsitans pupae*

Nash (1939) found in Northern Nigeria that female *G. morsitans* left a breeding-ground as soon as pupal mortality began to increase and that this coincided with rising soil temperature in the dry season and with rising soil moisture in the rains, but no explanation could be given as to what prompted the females to vacate a breeding-ground when they did. In 1942, however, he solved this problem by showing that the abandonment of the forest margin was not the result of any ability of the female fly to detect differences in the dryness of the air but to "a negative reaction to light developed by the whole community under conditions of universally high temperature", so that the period of migration to more suitable sites coincided with the time when shade temperatures approached the point at which Jack & Williams (1937) found the negative reaction to light began (about 90°F, or 32°C).

#### *G. swynnertoni*

Moggridge (1936a) conducted some experiments on the crossing of open spaces by *G. swynnertoni*. A party of five men and three oxen walking through long grass and under dry-season conditions failed to attract the fly from bush at a distance greater than 100 yards. The average number of flies attracted to a party passing the edge of fly bush at a distance of 100 yards was eight in 17 minutes.

Of a total of 61 flies caught on a 100-yard transect, 59 were taken off cattle. A marked preference was shown by the flies for two of the oxen; only 3.39% of the total were taken off the third ox.

Under conditions of excellent visibility in a similar set of five experiments made later in the dry season over ground which had been partly burnt, with a party of four men and three oxen, only 17 flies were caught. Of these, one was taken at a distance of 300 yards, four at 200 yards and 12 at 100 yards from the edge of the fly bush. The average time taken to complete the 100 yards patrol in this second set of experiments was 14 minutes. The flies were shown on two occasions to be in high density on the edge of the bush adjacent to the experiments.

Vicars-Harris (1936), working at Shinyanga in Tanganyika, studied *G. swynnertoni* in relation to various vegetation types and found that this fly appeared to concentrate in the hardpan during the latter part of the rainy season, the concentration reaching a peak at the end of the rains.

The fly then dispersed more and more into the shadier or better-grassed vegetation types as the dry season progressed.

#### *G. tachinoides*

Nash (1936) showed that the diurnal activity of *G. tachinoides* varied according to temperature and season, the fly becoming inactive below a temperature of 60° F (15.5° C) and again above 105° C (40.5° C); in order to avoid excessive temperatures, it settled on or near the ground in the shade of low thickets. Its activity was greatest between 81° F and 85° F (27.2°-29.5° C). In the hot weather it was most active in the mornings and evenings, whereas at the height of the rains activity was greatest at about mid-day (Glover, 1961b).

#### *G. palpalis*

In Northern Nigeria, Davies (1958) found that *G. palpalis* did not appear to be active as early in the morning as the other tsetse flies because he caught most of them between 11.00 and 14.00 hours, and on cloudy or hazy days they did not appear readily at any time.

Page (1959a), working in Southern Nigeria, found that during both the wet and dry seasons, "peak" densities of *G. palpalis* occurred between 12.00 and 15.30 hours.

#### *G. longipalpis*

Morris (1934), working on the Gold Coast (now Ghana), found that *G. longipalpis* was normally

inactive during the night but would appear in large numbers from 08.00 hours onwards until 12.00 hours, when they became less active, but from 16.00 hours until sundown they appeared in greater numbers again. The period of their maximum activity was between 10.00 and 11.00 hours.

#### *G. fusca* and *G. tabaniformis*

Studies by Jordan (1962b) in Southern Nigeria showed that the activity of *G. fusca* in the wet season varied little at different times of day, although peak activity appeared to be just before dark. In the severe conditions in the dry season in the riverine forest, activity was negligible between about 12.00 and 17.00 hours.

Analysis of the sex ratio of *G. tabaniformis* throughout the day showed that rather more than half of the flies caught before 07.00 hours and after 18.00 hours were males. During the middle of the day females greatly outnumbered males. On an ox fly-round, 58% of the catch of *G. tabaniformis* was females. From a tethered ox 65% in the wet season and 70% in the dry season of a mixed catch of *G. tabaniformis* and *G. fusca* were females (Jordan, 1962b).

#### ASSESSMENT OF TSETSE-FLY POPULATIONS

Glasgow & Wilson (1953) studied the tsetse-fly population on Nyalagobe hill on the shores of Lake Victoria by releasing and recatching marked flies along cut paths during the first three days of each of 16 weeks between April and July. They calculated that the population of *G. fuscipes* on Nyalagobe hill was 5000 and of *G. pallidipes* 50 000.

They also estimated the population of probable host animals as 43 by recording daily the tracks of different species of animals on the paths and by stretching two strands of cotton 12 inches and 24 inches (30 cm and 60 cm) from the ground along the uphill sides of the paths. The commonest animals were bushpig, of which there were 15; there were also 13 bushbuck. On the average, every animal supported 1163 *G. pallidipes*; and, if *G. pallidipes* fed once every four days, each animal must feed 291 *G. pallidipes* a day, or two of these flies every five minutes, assuming that the flies fed steadily throughout the 12 hours of daylight. Glasgow & Wilson further found that one *G. pallidipes* took up about 60 mg of blood per feed, so that each animal lost 17.5 g of blood per day.

Glasgow (1954), studying *G. fuscipes fuscipes* on the north-eastern side of Lake Victoria, made three

counts of its population in 50 acres (20 ha) of lakeside forest. He found that populations of *G. fuscipes* in this area showed long-term fluctuations which were not annual and not seasonal. On the lake shore the density of *G. fuscipes* correlated roughly with the width of the forest, being lowest where the forest was narrow.

In the widest piece of forest studied, which was a block 2200 yards (2011 m) along the lake shore by 100 yards (91 m) wide, the non-teneral male population was 4600. The mean catch along the 2200 yards of shore was 78 non-teneral males. This was more than 10 times the population which would be inferred from the same catch of *G. morsitans* or *G. swynnertoni*.

In this isolated block the mean death-rate of *G. fuscipes* was 26% per week and the mean length of life of the flies was 27 days.

Comparison of these catches with figures obtained from earlier studies of *G. fuscipes* in riverine vegetation in South Nyanza indicated that riverine *G. fuscipes* were always more hungry than those found on the lake shore, because the percentages of teneral flies, females and male, taken on the river were all higher than those on the lake shore. More female flies and fewer males were caught from a boat than on land. Carrying screens produced more female flies in the catches on some occasions but not on others. The reason for this discrepancy was not discovered.

Although this earlier work done by Glasgow (1954) in Nyanza Province of Kenya had led to the conclusion that riverine communities of *G. fuscipes* were permanently hungrier than lakeside communities, subsequent observations (Bursell & Glasgow, 1960) in the two types of habitat, in which a different area was used to represent the lakeside, showed that lakeside flies were slightly smaller than riverine flies and that they did not differ in the fat content.

A further investigation was made; puparia were collected on three occasions between January and March 1958 and their surface areas measured. In all samples the riverine puparia were significantly larger than those from the lakeside and the flies which emerged showed a comparative difference in size, but not in fat content corrected for size.

Estimates of the fat content of non-teneral flies in this experiment supported the conclusion that this lakeside community was under stress compared with the riverine community.

The reason for these results not agreeing with those described by Glasgow (1954) was thought to

be that the average temperature during February and March was 2°C higher at the site of the subsequent experiments than at the earlier.

These results suggested that the percentage of non-teneral male flies caught had a real meaning in terms of nutritional status and that it was also a very "responsive indicator", but that the proportions of teneral and female non-teneral flies might not be simply related to the nutritional state as had hitherto been supposed.

Later, Jackson (1955) designed a spiral fly-round to study *G. morsitans* game relationships at Daga Iloi in Tanganyika. He found that there was a positive correlation between the number of ungulates present and the hunger of the flies, but a negative one between the number of ungulates and the number of flies. This method was also used by Harley to assess the tsetse-fly population of Waturi peninsula (Fryer, Johns & Yeo, 1957) and by Johns (1958) for the same purpose on Sikiri point and a part of the Ruma bush in the Lambwe valley in South Nyanza. Weitz et al. (1958) used a similar method with some modifications in Kenya and so did Langridge (1960a, 1961) in his studies of tsetse-fly host preferences.

Glasgow (1961d) showed that two species of East African *Glossina* have characteristic sizes which vary very little. This is a result of adenotrophic viviparity, but there are examples in the literature of differential mortality causing samples of adult wild flies to be even less variable than those emerging from wild pupae.

Large samples of wild *G. morsitans* and wild *G. swynnertoni* were compared with samples emerging from puparia collected in the same area. During a period of four months it was observed that populations of wild *G. morsitans* were losing about 12% of their smallest members, the effect disappearing towards the end of the dry season.

Male *G. swynnertoni* populations did not undergo differential mortality, and 34 taken as the prey of Asilidae showed no size bias. Female *G. swynnertoni* populations, on the other hand, did show differential mortality and both the large and smaller individuals were eliminated by unidentified causes, so that a female of the mean size had the greatest expectation of life.

Harley (1958), working in two areas in Ankole, Uganda, obtained estimates of the standard availability of *G. morsitans morsitans* which gave the maximum and minimum fiducial limits of 2.0% and 0.19%. These were much lower than the estimates

of approximately 10% obtained by Jackson in Tanganyika. This difference was of practical importance in that a single fly caught in Ankole indicated a much larger population than a single fly caught in Tanganyika, which was the probable explanation for the trypanosomiasis problem around the edges of the fly-belt in Ankole, where routine catches revealed very few flies.

Ford (1958) had reported that tsetse flies followed the catching parties for some distance from a high fly-density area before being caught, thus giving a misleading picture of their true distribution.

Ford et al. (1959) described a modification of the fly-rounds laid out according to vegetation types in an area which had been used for a long time in the study of *Glossina*. This new "transect fly-round" made it possible to collect much more detailed information, particularly on the distribution of tsetse flies.

Glasgow (1961b), investigating the variability of fly-round catches, found, surprisingly, that in a comparison of day-to-day variations of *G. swynner-ioni* catches, the transect fly-round was no better than the old type. The variance on the transect fly-round was greater than could be accounted for by random errors and must be the result of changes in availability of the fly as the population would be unable to fluctuate so widely in so short a time.

Welch (1958), investigating the diurnal variation in catches of *G. morsitans orientalis* in Tanganyika, showed that the first traverse of a fly-round, almost irrespective of the time of day, made the highest catch. This confirmed Jackson's results (1930) and should be taken into account when early morning peaks in fly activity are discovered.

Isherwood (1958), working in the Mitoma county of Ankole, Uganda, observed that the availability of *G. fuscipleuris* was very low on nine morning traverses with bait oxen; 117 male flies and 145 females were caught. On nine traverses made along the same fly-round without bait oxen, three in the morning, three in the afternoon and three in the evening, only two male flies and five females were taken.

Morris (1960a) used his "animal" trap to study the habitat and host relationships of *G. pallidipes* in an area in Uganda where this fly was the vector of *T. rhodesiense* sleeping-sickness (MacKichan, 1944; Morris, 1958). He found that this type of trap caught more flies and gave more truly representative samples of the tsetse-fly population than did either fly-boys or Chorley's bicycle screen.

Black traps were generally better than brown traps, this superiority being greatest in the wet season and disappearing in the dry season. The explanation for the variations in the catching ability of these traps was thought to be that the tsetse fly was attracted to them because it mistook them for a natural host.

A trap double the linear dimensions of a standard trap caught three times as many flies.

Because trapping gave a standard measure of fly incidence, which allowed for catches at different times and places to be compared, it was used to determine the habitat preferences of *G. pallidipes*, its periods of activity throughout 24 hours and the influence of the presence of its host animals.

In a squatters' settlement in a belt of *G. pallidipes* in a closed sleeping-sickness area in South Busoga, trapping produced a striking reduction in the numbers of tsetse flies during the first eight weeks, which was explained by there being resident "anthropophilous" flies within and around the settlement which the 18 traps in operation rapidly caught. After the first reduction in numbers, flies coming into the settlement in very small numbers continued to be caught. Surprisingly, more were caught in open cultivated fields of low crops and in the open compounds of the houses than in the apparently more attractive cover of shady banana plantations.

The fact that settlement automatically lowered the numbers of tsetse flies in the immediate surroundings, compared with an undisturbed fly belt, supported the possibility of reclaiming a strip of country from *G. pallidipes* by means of settlement alone.

The use of traps demonstrated that marked and local reductions in fly incidence took place when the South Busoga settlement scheme was put into operation and provided information of value for wider developments on similar lines.

Smith and Rennison (1961a) caught *G. pallidipes* on bait oxen, in Morris traps and on a fly-round operated by two fly-boys in south-eastern Uganda. Fewer flies were caught in traps than on bait oxen but traps caught a higher proportion of females. Traps covered with natural-coloured hessian took more than those with hessian painted black. A white bait ox attracted fewer flies than a darker-coloured one, and a red ox was most attractive. Variations in diurnal conditions and site indicated that the sexes were differently affected by these factors. Data obtained from the fly-rounds appeared to give an unsatisfactory estimate of the population density.

The numbers caught by the various methods did not correlate and this cast doubt on the validity of fly-rounds or trap data as reliable estimates of the number of *G. pallidipes* likely to attack cattle.

In a further paper, Smith & Rennison (1961b) described catches of *G. pallidipes* made at 1½ hour periods between 08.00 hours and 18.30 hours daily, during two experimental periods, in the early wet season of 1957 and the late dry season of 1958, using small East African zebu oxen, Morris traps and standard fly-round techniques. The flies were attracted in greater numbers to the oxen in the morning and evening than at midday, the evening increase being most marked in the wet season. Daily catches of both sexes of the fly on oxen, though starting at much the same point in both seasons, fell to lower levels at the hotter times of day during the dry season and rose very slightly in the evening. Traps, on the other hand, in both seasons caught most females between 12.30 and 14.00 hours and least in the mornings. Male flies were trapped in greatest numbers between 14.00 and 15.30 hours in the wet season, but in only comparatively small numbers at any time in the dry season. There was a suggestion of maximum availability occurring between 11.00 and 12.30 hours during the latter. During the dry season catches on the fly-rounds and on bait oxen showed a similar periodicity in female availability, with a peak from 09.30 to 11.00 hours.

Smith & Rennison (1961c), in two further experiments in south-eastern Uganda, found that when non-teneral male *G. morsitans* were caught concurrently on oxen and in Morris traps and classified within 1½ hours of capture according to the hunger stages described by Jackson (1933a), there was a marked difference between the assessments of individual recorders. Therefore no conclusions regarding the hunger stage of flies taken by different attractants could be drawn from the first experiment.

In the second experiment, however, which was so designed as to discount possible bias among recorders, the proportion of "hungry" flies (stages 3 and 4) in male catches were similar on individual oxen of various colours, and generally higher than in trap catches, in which there was a wide variation in the proportions. As all the traps appeared identical, no generalization could be made about the mechanism by which non-teneral male flies were attracted to and induced to enter these traps.

Continuing their experiments in south-eastern Uganda, Rennison & Smith (1961) showed that the catch of *G. pallidipes* by Morris traps was not

significantly affected by varying the interval between emptying the traps within the range of 1½ to 24 hours or by varying the width of the entrance slit from ¼ to 1¼ inches (6-32 mm).

Almost no flies were caught in the traps between 18.30 hours and 06.30 hours.

Traps with simulated defects such as leaving the sleeve open or making holes in the cage gauze caught fewer flies than perfect traps. The diameter of the sleeve-opening did not affect the catch but 16 half-inch (13-mm) holes in the cage gauze affected it significantly compared with 2, 4 and 8 holes.

When the interval between emptying traps exceeded 24 hours, losses of trapped flies occurred as a result of predation by ants.

This was thought to be the most likely cause of significant variation in catches between apparently identical traps. When the traps were mounted on greased single legs, however, there was no significant difference in catches between those cleared at intervals ranging between 12 hours and 8 days.

The median length of life of flies captured in traps was about two days.

Bursell (1961) determined the fat content and residual blood meals of tsetse flies sampled in four different ways: by standard catching parties, from resting catches, from catches from bait animals, and from catches from vehicles. He found that the fat content of male flies containing blood in late stages of digestion was high for the standard catch, low for resting and bait-animal catches, and intermediate for vehicle catches. The females caught showed an opposite trend, the fat content being low in the standard catch, high in the resting and bait-animal catches and intermediate in the vehicle catches. These findings were interpreted in terms of changes in the behaviour of flies in the course of the hunger cycle. Four phases were recognized in the male hunger cycle:

- (1) phase of inactivity;
- (2) phase of activity characterized by sexual appetitive behaviour;
- (3) phase of activity characterized by appetitive behaviour in relation to feeding reaction, but by indifference to the stimulus of moving objects;
- (4) as for (3) above, except that moving objects constituted an adequate stimulus for the release of the feeding reaction.

The bearing of these results on the problem of "host preferences" and the possibility that quiescence and shade are important components of the

stimulus conditions which control the feeding reaction in tsetse flies might go some way towards explaining the striking discrepancy between the apparent availability of different species of potential host animals in a tsetse-fly habitat, and the frequency with which they are fed on by tsetse flies.

Glasgow & Bursell (1961) described the results obtained from studying a population of *G. swynner-toni* at Shinyanga in Tanganyika in respect of size and fat content by monthly samples over a period of 13 years.

These results showed that the flies were large from February to July and small from August to January. This change in size suggested an effect of the wet season, which lasted from December to May, upon the parent females. Male flies had more fat in the rains and less in the dry season, and Glasgow & Bursell thought it possible that similar changes in the nutritional status of females were responsible for the observed size changes.

#### EFFECT ON TSETSE FLIES OF ARTIFICIAL CHANGES IN THE HABITAT

Glasgow & Duffy (1951) attempted to exterminate a population of *G. fuscipes* by hand catching on the Kuja River in Kenya in 1½ miles of riverine forest separated from other riverine bush by clearings 2 and 3 miles wide on either side. They found that more *G. fuscipes* could be caught from boats on the river than from paths beside the river. They twice attempted to prevent the fly from crossing the clearings, firstly by stretching DDT-treated hessian screens right across the river and secondly by placing large numbers of "trap-screens" treated with DDT in the clearings, but neither method had a decisive effect.

Wilson (1953), commenting on various methods used for the eradication of *G. fuscipes* in Kenya, said that hand catching of *G. fuscipes* had the most limited application.

He reviewed the effects of total and discriminative bush clearings on the Yala, Migori and Nyando rivers of Nyanza and remarked that the decrease in fly population caused by these clearings was gradual but complete eradication might be achieved. The maintenance of these clearings was difficult, the initial cost varied from £200 to £300 per mile and labour was often hard to obtain. However, the use of 5% DDT sprays on the fringing vegetation along 20 miles (32 km) of the Mbogo river in Central Nyanza had given dramatic results and *G. fuscipes*

had been eradicated in this area at a cost of only £42 per river mile. This was the beginning of one of the most successful campaigns ever undertaken against *G. fuscipes* (Fairclough & Thomson, 1957; Burnett et al., 1957; Glover et al., 1958).

That it was possible to exterminate *G. fuscipes* from isolated patches of riverine bush in Kenya had been proved by Symes & Vane (1937) and later by Glasgow & Duffy (1947).

Langridge (1956), investigating the climatic factors influencing the choice of habitat by *G. austeni* on the Kenya coast, found that, when the habitat was modified by removing certain elements of the vegetation to admit brighter light than that existing under natural conditions, a state of hyperactivity was produced in the fly which reduced its fertility and resulted in ultimate exhaustion and death. Also a daily maximum temperature of over 30°C produced infertility in the fly, if maintained for a long time, but high atmospheric humidity did not appear to be as important to *G. austeni* as light intensity and temperature.

In response to a request by the Government of Northern Rhodesia in 1935, the Tanganyika Department of Tsetse Research established fly-pickets at various points on roads and paths entering the European farming area in the Abercorn district in 1936; in addition a belt of country was protected from fire, in order to thicken the woody vegetation and so make it unfavourable as a habitat for *G. morsitans*. The fire-protected area was extended and continued until 1946 but serious escape fires occurred in 1938 and 1941. As a result of protection from fire during the first five years, the catches at the pickets were reduced by about one-third.

In 1941 several shallow valleys forming the headwaters of small tributary streams where concentrations of *G. morsitans* existed were cleared of trees and the apparent density of the fly was at once reduced, not only in the valleys themselves, but over large areas of untouched *Brachystegia* woodland round about. These clearings were extended to new fly concentrations as they were discovered until 1952.

From these experiments it was concluded that fire exclusion alone was not a quick means of reducing fly numbers but that the total area of discriminative clearing was less than one-third of the experimental area, which covered 280 square miles (725 km<sup>2</sup>). It was not known how this worked (Glover et al., 1955). Experimental discriminative clearing was also carried out in the Tabora district of Tanganyika,



as reported in the annual reports of the East African Tsetse and Trypanosomiasis Research and Reclamation Organization for 1950-52.

Bursell (1955) delimited a recent extension of a fly-belt in the Songea district of southern Tanganyika. He also showed that the preferred habitat of *G. morsitans* in this region consisted of "short-grassed glades representing old village sites, in well-grown *Brachystegia* woodland with a double canopied inter-zone between glade and woodland". He thought that the destruction of the inter-zone by clearing the upper canopy would undoubtedly prove effective in causing eradication of the fly.

The situation following different degrees of discriminative clearing against *G. morsitans* Westwood was examined by Harley & Pilon (1961) in the eastern Ankole district of Uganda. In one area, where the treatment had been most intensive, the fly density was low, and it seemed that the population might be maintained by immigration from an adjacent area to the west where clearing had been less drastic and in parts of which the fly density was relatively high. More intensive discriminative clearing of fly concentration sites in the western area, together with the completion of treatment of the eastern area, failed to produce any marked effect on the tsetse-fly population except in its distribution. Before intensive clearing was begun, *G. morsitans* occurred in a double-storey vegetation type, the chief component of the upper story of which was *Acacia gerrardii*. After the upper-story trees were felled, fly concentrations were found in groups of tall *Acacia hockii* 12-18 feet (3.6-5.5 m) high, which had appeared to be unimportant to the fly before clearing started. A year after the treatment of the western area there was no apparent reduction in fly density.

The failure of this discriminative clearing experiment in Ankole might render Bursell's statement on the clearing of the upper canopy of the inter-zone in Songea less certain.

#### GAME DESTRUCTION

There has been much controversy regarding game destruction as a practical means of tsetse-fly control, particularly as a result of the operations in Southern Rhodesia (Chorley, 1947), and later in Uganda (Uganda, Tsetse Control Department, 1950-60).

The present status of game destruction as a means of controlling trypanosomiasis has been dealt with

by Hocking, Lamerton & Lewis.<sup>1</sup> Game destruction judiciously applied has been, and still may be, under some conditions, both economical and practical for trypanosomiasis control. However, modern developments in tsetse-fly control, mostly chemical, have already shown that under most circumstances they are as effective and as cheap as game destruction, and they will probably be even more efficient as time goes on. Further, the preservation and exploitation of game has been shown to be profitable and, for these reasons, most countries which practise game destruction for the control of trypanosomiasis are substituting other methods. The status of game destruction is in rapid decline and that decline may be expected to continue.

#### MAN-FLY RELATIONSHIPS

Glasgow (1960) indicated that the presence of tsetse flies denied about a quarter of the African continent to domestic stock. Tsetse flies were creatures of woodland, unable to exist in open pasture of arable land and therefore they could be eliminated by clearing the bush. The difference between bush clearing as an essential prerequisite to human occupation and bush clearing as a means of tsetse-fly control were differences of detail only.

The over-all picture of the *G. morsitans* infestation in Northern Rhodesia is one of a fly population recovering from the setback it received after the great rinderpest epizootic and other influences which swept East and southern Africa at the turn of the century.

In its attempts to recolonize land from which it has been ousted, a variety of circumstances either natural or man-made, have retarded its advance. The infestation can now be divided into six geographical belts. In the main these consist of large uninhabited or sparsely populated areas devoid of livestock and with an interrelated game-fly complex. They are interspersed with areas of denser human population concentrated around urban or semi-urban communities. These are not large enough to occupy or exclude the fly from the country it inhabits, but only to check further encroachment, except around the Copper-belt and in the vicinity of Broken Hill Mine township, which were infested with fly before the country was opened up by the mining communities.

Within the tsetse-fly-infested areas the people live in small scattered communities existing at sub-

<sup>1</sup> See the article on page 811 of this issue.

sistence level but maintaining an uneasy balance with their environment by practising shifting cultivation and augmenting their requirements by hunting, fishing and collecting natural forest products. Over most of Northern Rhodesia, population pressure demanding more land is only localized, and consequently tsetse-fly control operations are aimed at the protection of existing settlement rather than at providing more land for occupation by a surplus population.<sup>1</sup>

The situation in Southern Rhodesia is much the same. Here there is an over-all human population density of 19 to the square mile (7 per km<sup>2</sup>) or 22 per square mile (8.5 per km<sup>2</sup>) in tsetse-free country.

Similarly, in Tanganyika there is an over-all population of 25 people to the square mile (9.6 per km<sup>2</sup>) and 67 (26 per km<sup>2</sup>) in tsetse-free country.

In Northern Nigeria, Nash said that *G. morsitans* usually occurred in areas where the human population density did not exceed 0-40 people per square mile (0-15 per km<sup>2</sup>); occasional light infestations might occur where there were 50-100 people to the square mile (19-38.6 per km<sup>2</sup>), but never in places more densely populated than 100 to the square mile (Glover, 1961b).

Nash (1948), discussing man-fly relationships, said that the time of concentration of *G. palpalis* varied with different streams, the dry reaches being vacated first in favour of the vicinity of the permanent pools; then movement up and down the stream ceased. Should a village be near these pools, as frequently happened, the man-fly contact became very close, the same flies biting the same people each time they came down the pools. He described this as close "personal" contact. The situation in which the members of a fairly large fly population moving up and down a stream in mild years bite people in passing, but seldom bite the same person again, he called "impersonal" contact. This is a very important factor in the epidemiology of sleeping-sickness in Nigeria.

In Nyasaland, human population is a most notable controlling agent with an over-all density of 89 per square mile (34 per km<sup>2</sup>) and 97.5 (37.7 per km<sup>2</sup>) for tsetse-free land. Elsewhere in Central Africa only on the coast of Mozambique does the population over fairly large areas reach more than 100 to the square mile.<sup>2</sup>

The over-all population per square mile in Uganda is about 80 (31 per km<sup>2</sup>) but in parts of Buruli county it is as much as 174 (67 per km<sup>2</sup>) and, in the Mengo district of Uganda, 134 (52 per km<sup>2</sup>).

In Kenya the over-all population is about 30 per square mile (12 per km<sup>2</sup>), but in the Central Province it is 181 (61.9 per km<sup>2</sup>) and in Nyanza 194 (97.9 per km<sup>2</sup>); in fly-free country generally it is about 60 per square mile (23 per km<sup>2</sup>); in the fly-infested country it is about 15 per square mile (5.8 per km<sup>2</sup>) but in the Northern Province as a whole it is only 1.5 (0.6 per km<sup>2</sup>).

Fundamentally, the tsetse-fly problem in East Africa is not very different from that in Central Africa in that in most cases fly control operations are aimed at the protection of existing settlement.

In Kenya several areas have been freed of fly for human settlement in the past ten years by means of bush clearing, both by hand (Glasgow & Duffy, 1959) and with machines (Glover et al., 1959), but in most cases the indifference of the local inhabitants to the maintenance of these clearings has rendered the control of regrowth too costly for this method to be used on a large scale.

On the other hand, the use of insecticides on isolated areas where reinfestation by the fly is impossible after it has been exterminated has proved very promising, and it is this field of control which is likely to benefit most from advances in our knowledge of the ecology of tsetse flies.

At this stage we feel it necessary to sound a note of caution. The extermination of tsetse flies and the diseases they carry may be a laudable end in the cause of humanity but the past 30 years of tsetse-fly control work in East Africa have shown that the emphasis lies on *control*. There is little point in clearing large areas of tsetse-infested bush merely to allow it to grow up again and become reinfested with fly or so damaged by misuse that the soil is eroded away.

Large-scale schemes for the reclamation of land from tsetse flies should be undertaken only where proper land use is assured and complete control of the flies guaranteed by the co-operation of the people themselves. Otherwise it is better to leave them alone.

In many parts of Kenya which are over-populated either by man or by his stock or by both, man is so dangerously out of balance with his environment that he is barely able to scrape a meagre living at subsistence level. This situation has arisen, not because there is not enough land for everyone nor

<sup>1</sup> Data sent to us (1962) by W. S. Steele for inclusion in this paper.

<sup>2</sup> Data sent to us (1962) by J. Ford for inclusion in this paper.

because the land is denied to the people by tsetse flies, but because of the present methods of land use and stock management; "Pax Britannica" and the enormous impact westernization has had on indigenous populations have brought undreamed-of medical facilities and other benefits but have by no means controlled and stabilized expanding human populations.

A very good example of the effect of man's imbalance with his environment in East Africa is the result of three years' drought which ended in 1961. In the Kajiado district of Kenya alone more than 60% of the Masai cattle died. The drought was followed by floods, with the result that a large proportion of the population of Central Kenya, Masailand and the Coast Province had to (and many still have to) rely on famine relief for their very existence.

It is well known that the presence of game animals and dense agricultural populations are incompatible unless a conscious effort is made to preserve the animals in national parks and other sanctuaries.

Glasgow (1960) said that tsetse flies in tropical Africa encouraged the development of intensive systems of land use so that human beings were concentrated in the minimum area and the prospects for wild animals which lived in the areas not required by human beings were thereby improved. This statement may be true under special circumstances involving highly organized and civilized communities but in most parts of Africa it is the very density,

poverty and conservatism of the expanding populations that constitute the gravest threat to man himself and to all other living things—not the tsetse fly.

In conclusion, we quote an extract from the opening address of the Governor of Tanganyika, Sir Richard Turnbull, K.C.M.G., to the CCTA/IUCN Symposium on the Conservation of Nature and Natural Resources in Africa, held at Arusha in September 1961:

"Man is the most dynamic biological factor which has ever disturbed the balance of nature on earth, for he has ceased to be an integral part of the environment and has become a controlling factor, disturbing by one means or another the natural balance of other living things. Man and his stock, however, still increase unchecked. Geological changes, sun spot cycles, solar radiation, wind rainfall and temperature are beyond man's control, but the preservation of soil and shelter is not."

In spite of the fact that a quarter of the African continent is denied to domestic stock, man and his animals multiply unchecked to bring about their own ultimate destruction by ruining for ever the land they live on. The fallacious belief that in Africa land is inexhaustible and put there for man to exploit at will cannot fail to lead to disaster.

The preservation of the land and the problem of saving mankind from self-annihilation are no longer scientific issues, but social and political ones demanding the urgent attention of the educationist and the statesman.

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## RÉSUMÉ

Les auteurs passent en revue les acquisitions récentes concernant l'habitat et la répartition géographique des vecteurs principaux de la trypanosomiase dans les régions non francophones de l'Afrique orientale, centrale et occidentale. Tous ces problèmes — et plus particulièrement ceux relatifs à la répartition, aux modes de vie, aux mécanismes d'adaptation des différentes espèces de mouches tsé-tsé — ont fait l'objet ces dernières années de nombreuses et fructueuses recherches de la part des

entomologistes, des géologues, des géographes, des agronomes, des zoologistes aussi bien que des médecins ou des parasitologues.

Les recherches ont surtout porté sur la biologie de la mouche elle-même (en particulier sur ses besoins en eau) et sur les réserves de graisse des nymphes. Celles-ci sont insuffisantes lors des baisses de température; ainsi s'expliquent les limites méridionales de l'habitat de *Glossina morsitans* en Afrique.

Des changements sont intervenus, depuis quelques années, dans la répartition géographique des mouches tsé-tsé; elles ont envahi certaines vastes régions, évacué d'autres. L'avance de *G. morsitans* en Rhodésie du Sud a été telle qu'une inquiétude réelle s'est emparée des autorités sanitaires de cet Etat.

La généralisation de l'emploi des insecticides résiduels a incité les entomologistes à étudier la façon de vivre — et, en particulier, de se reposer — de la mouche tsé-tsé. Une telle connaissance est indispensable à la mise au point de méthodes à la fois efficaces et économiques dans la lutte contre l'insecte.

Depuis longtemps déjà l'on s'est intéressé aux gîtes de la tsé-tsé, essentiellement dans le but de détruire directement l'insecte mais aussi dans l'espoir d'une lutte biologique (par l'intermédiaire de parasites).

D'intéressantes recherches ont porté sur les prédateurs ou parasites éventuels des mouches tsé-tsé. L'on a souvent

observé l'absence de nymphes dans des endroits tels que végétaux en décomposition ou arbres morts, tout à fait indiqués pour servir de gîtes. L'on pense que cette absence peut être due, entre autres choses, à leur destruction par les fourmis. Les *Asilidae* s'attaquent surtout à *G. swynner-toni* adulte.

En Rhodésie l'on a étudié chez *G. pallidipes* les habitudes alimentaires qui changent au rythme des saisons. *G. longipennis* semble particulièrement vorace au crépuscule. D'autres espèces de tsé-tsé s'alimentent de façon différente, et ces variations sont le plus souvent sous la dépendance de facteurs climatiques.

En terminant, les auteurs insistent sur les moyens de lutte contre les mouches tsé-tsé; cette lutte ne pourra se terminer par la victoire de l'homme que si l'on connaît d'abord à fond la biologie de ces insectes vecteurs et leurs moyens d'adaptation au milieu géographique (sol, climat, végétation, faune).

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